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# AFFERENT INFLUENCES ON TONGUE MUSCLE ACTIVITY

## A Morphological and Physiological Study in the Cat

By

SIGFRID BLOM

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# Preface

This investigation was carried out at the Department of Anatomy, University of Uppsala, Uppsala. The author wishes to thank the Head of the Department, Professor Bror Rexed, for the laboratory facilities which he has provided, for the interest he has shown in the investigation and for valuable criticism.

Docent Sten Skoglund originally interested me in the problems of tongue muscle innervation. I am greatly indebted to him for initiating me into neurophysiological technique and for his never failing interest in discussing the difficulties of various kinds met with during the investigation. The stimulating atmosphere in his laboratory has meant very much to me during my work there.

I also wish to thank my present chief, Professor K.-A. Ekbom, for valuable help.

I am grateful to Docent K.-E. Hagbarth for his kindness in reading the manuscript and for valuable discussing.

Fil. mag. Rolf Lundgren has corrected the English text.

Finally, I want to thank my colleagues and the technical staff of the Institute for much help and assistance.

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Uppsala, march 1960.

*Sigfrid Blom*

# General Introduction

The nerves which contribute to the somatic innervation of the tongue have long been well known. This innervation is shared between the hypoglossal, the lingual and the glossopharyngeal nerves. To the general somatic afferent fibres of the two last-mentioned nerves are added general and special (efferent and afferent) visceral fibres. The hypoglossal nerve, on the other hand, has been held to be a purely motor one, that is to say: its components have been thought to be efferent only. From the time when the significance of the proprioceptive innervation for muscle function in general was elucidated, the question of the arrangement of the innervation of the tongue in this respect naturally arose. This problem is interesting also because the hypoglossal nerve does not have a posterior root comparable to that of the spinal nerves. From the embryological point of view, the nerve has long been held to be equivalent to the spinal nerves, its nucleus being a rostral prolongation of the ventral cell column of the spinal cord.

Many investigations have been performed with the intention of finding out what afferent sources the hypoglossal nucleus has at its disposal and also if the sense organs in the tongue, giving rise to the afferent impulses acting upon the hypoglossal nucleus are the same as in other striated musculature, for example that of the limbs, i. e. the muscle spindle and the Golgi tendon organ. In the investigations earlier performed both morphological and physiological methods have been used. The results have been contradictory which will be quite obvious from the survey of the literature. The earlier physiological experiments in this field were performed before the fundamental mechanisms of the proprioceptive innervation in general were known, a fact which

made the judging of the results difficult and uncertain. In some cases they led to conclusions which must now be revised.

The investigation to be presented in this work is a study of the innervation of the tongue with respect to the following main points:

1) Are muscle spindles present in the tongue muscles?
2) The afferent pathways for impulses from the tongue and other structures acting upon the hypoglossal nucleus.
3) The way in which the afference from the tongue acts upon the hypoglossal nucleus as revealed by a study of the efferent activity in the hypoglossal nerve and the tongue muscles.

It is not possible to obtain complete and reliable information on this problem without using both morphological and physiological methods. It is then for obvious reasons desirable to use the same species for both types of investigation.

# Survey of the Literature

Earlier work on the problem of the proprioceptive innervation of the tongue has mainly consisted of a search for sensory nerve endings in the tongue muscles and furthermore studies of the hypoglossal nucleus, the nerve with its connections. In this survey only the hypoglossal nerve, and not the morphology of the tongue will be dealt with. Earlier results concerning the stretch receptors in the tongue are going to be surveyed in connection with the description of the author's own investigations in this matter.

CAJAL (1909) found the cells of the hypoglossal nucleus very similar to those in the ventral horn of the spinal cord. BOYD (1941), who worked with rabbit embryos, stated that it was not possible to distinguish between the cells of the hypoglossal nucleus and the motor cells of the upper cervical nerves. The same fact was pointed out by, among others, BARNARD (1940) and KIMMEL (1940). By cutting the hypoglossal nerve and studying the retrograde cell changes in the nucleus (of the dog) BARNARD (1940) also came to the conclusion that the cells are somatotopically arranged and so did VAN DER SPRENKEL (1924) studying serial sections of a hedgehog embryo. BARNARD also found that the nerve cells of the nucleus are unequal in size, those belonging to the so-called ventral group being larger than the others. He moreover found from his studies of retrograde degeneration that the geniohyoid muscle derives its innervation from the hypoglossal nucleus.

It is generally accepted that the small so-called perihypoglossal nuclei (nucleus intercalatus, nucleus prepositus and Roller's nucleus), which are situated in the vicinity of the main hypoglossal nucleus, do not contribute to the root fibres of the hypoglossal nerve. For further information regarding these

nuclei the reader is referred to a review by JANSEN and BRODAL (1954).

The non-existence of a dorsal root of the hypoglossal nerve (long known) has been the subject of some investigations. According to FRORIEP and BECK (1895), however, a root ganglion of small size is sometimes found. LANGWORTHY (1924, b) reported his finding of a ganglion in 24 out of 28 roots examined in 14 cats. The last-mentioned author made a histological examination of one of the ganglia belonging to these roots and stated that "they contain a few large myelinated fibres, surrounded by many unmyelinated". He expressed the opinion that this ganglion cannot contain all the cells subserving the proprioception of the tongue. HOLLIGER (1955) also found hypoglossal root ganglia in the cat in a few cases. On the other hand neither BOYD (1937 and 1941) nor KIMMEL (1940) was able to find any trace of a ganglion in the rabbit. In a comparative study (1940), BARNARD came to the same negative result.

Sensory cells localized along the course of the hypoglossal nerve have also been reported by some investigators. PEARSON (1939, 1943 and 1945) performed a series of studies on human embryological and adult material in part concerning sensory cells along the intramedullary course of the nerve. In the first of these works, performed on embryos, he suggested that the original dorsal root and ganglion of the hypoglossal nerve are incorporated in the accessory nerve and that the axons in question via the vagus nerve join the hypoglossal nerve. However, the study from 1943 revealed "sensory type neurons" along the intramedullary course of the twelfth nerve. These cells were not found along all the hypoglossal fibres transversing the medulla of the embryos studied but they were found in every case examined. In the work published in 1945, PEARSON performed the study on adult material. In this case, the cells were not so easy to find, they were partly unipolar, partly bipolar and sometimes represented transitional forms between these. The author claimed to have found that the axons from these "sensory type" cells followed the root fibres of the hypoglossal nerve. In this connection it is of some interest to note, that BOYD (1941) in his work on the hypoglossal nerve in rabbit

embryos also found intramedullary cells along the neurites of the nerve. This author, however, stated that the cells found by him were typical motor ones and he was of the opinion that their axons do not join the nerve. BARNARD (1940) remarked that the big cells of the ventral cell group, which are destined for the geniohyoid muscle, sometimes could be traced along the root fibres of the nerve in its intramedullary course. CAJAL (1909) evidently did not see any cells of this type. It is not possible to tell whether the above-mentioned authors are referring to the same cells in their publications. In any case, PEARSON expressed the opinion that the cells described by him might be sensory in function and probably proprioceptive. The existence of these cells has been called in question by CASASCO (1951), who holds them for staining artifacts, since he was not able to find them in preparations stained with Nissl, Giemsa or haematoxylin-eosin.

Sensory cells have also been sought for along the extramedullary course of the nerve. TARKHAN (1936, a) found a ganglion just at the origin of the descendent ramus of the nerve. Out of one degeneration experiment he drew the conclusion that the ganglion cells sent their neurites to the hypoglossal nucleus. Later, BOYD (1937 and 1941) sought for such ganglion cells along the nerve in the same specimen (the rabbit), but without finding them. This was also the outcome of the studies by CARLETON (1937) and LAW (1954). TARKHAN later made a more extensive study (TARKHAN and ABD-EL-MALEK 1951), using cats, dogs, rabbits, rats and human material and reported his finding cells in somewhat varying number and location along the nerve. FITZGERALD and LAW (1958) could not find any cells along the hypoglossal nerve in the pig.

To conclude, both TARKHAN and PEARSON are evidently of the opinion, that the nerve cells described by them are sensory in nature and proprioceptive in function. Their opinion is based on morphological studies only and apparently on the assumption that there are muscle spindles in the tongue.

One of the leading ideas concerning the proprioceptive mechanism of the tongue muscles has been that the afferent components leave the hypoglossal nerve somewhere along its

peripheral course and reach the central nervous system through some other nerve. Especially the upper cervical nerves have been supposed to constitute this pathway. Different species and different methods have been employed in investigations performed with the intention to find this route. The upper cervical nerves have been cut and after a proper degeneration-time degenerated fibres in the peripheral part of the hypoglossal nerve have been looked for. The first study of this kind was performed by HINSEY and CORBIN (1934). They removed, using the cat as experimental animal, the dorsal root ganglia C 1–C 4, but did not (after 10 to 22 days of degeneration-time) find any evidence of degeneration in the hypoglossal nerve. In 1937, however, CORBIN, LHAMON and PETIT in similar experiments performed on the rhesus monkey, reported a degeneration of between 1 and 2 % of the fibres in the hypoglossal nerve after removal of the second and—in one case—also the third dorsal root ganglion. This caused CORBIN and HARRISON (1938) to make a reinvestigation of the matter in three cats (direct osmium method, degeneration-time 9 days) with the same result as that reported by HINSEY and CORBIN 1934. The findings in the rhesus monkey reported in 1937 were in 1939 confirmed by CORBIN and HARRISON in experiments with section of the ventral rami C 2–C 4 and the same year YEE, HARRISON and CORBIN made a new study, this time using the rabbit. Removal of the first dorsal root ganglion in this animal showed a degeneration of 1 to 5 % of the fibres in the hypoglossal nerve. In this last-mentioned work, a somewhat longer degeneration-time was allowed and besides the direct osmium method the Marchi method was also used. TARKHAN (1936, a) had not in the same type of experiment made on two rabbits found any degeneration in the hypoglossal nerve. This author, however, performed his operation more peripherally and sectioned the anterior branches of the spinal nerves C 2–C 4.

CORBIN and HARRISON (1938) in the above-mentioned study also reported some physiological experiments and found "for proprioceptive impulses characteristic activity" in the ventral C 1 ramus, when the tongue was pulled so hard that the infrahyoidal musculature was stretched. DOWNMAN (1939) stimulated the

central end of the cut hypoglossal nerve in the cat, using dilatation of the pupil and rise of the blood pressure as an indication of afferent impulses and found that the activity obtained did not disappear when the dorsal root ganglions C 1 and C 2 were removed.

The possibility that the proprioceptive impulses from the tongue reach the hypoglossal nucleus via the cervical nerves was also treated in the morphological studies by VAN DER SPRENKEL (1924) and PEARSON (1939). These authors, the former using the hedgehog and the latter human material, describe connections between the cervical nerves and the hypoglossal nerve. VAN DER SPRENKEL reported axons from cells, located in the ganglion of C 2 joining the ramus descendens of the hypoglossal nerve and conducting proprioceptive impulses from mm thyreohyoideus, hyoglossus and styloglossus. PEARSON observed fibres running with the ramus descendens hypoglossi from C 2 and turning back again to the hypoglossal nerve. A proprioceptive function of these fibres was only supposed by these authors.

Shortly after its exit from the skull the hypoglossal nerve lies in close proximity to the glossopharyngeal, vagus and accessory nerves. Connections are established especially with the ganglion nodosum. In current text-books of anatomy (i. e. RAUBER-KOPSCH 1955, CLARA 1953) is stated that nerve fibres pass from the vagus to the hypoglossal nerve here; these fibres are supposed to be autonomic and designed for the innervation of the heart, thus evidently leaving the main hypoglossal trunk again. BOYD (1941) made a study in the rabbit of these supposed fibre-exchanges, but did not find any evidence of their existence. TARKHAN and ABOU-EL-NAGA (1947), on the other hand, removed the ganglion nodosum in dogs and found 5 % degeneration in the peripheral part of the hypoglossal nerve. A description of the hypoglossal nerve and its branches is found in the works by ABD-EL-MALEK and BARNARD 1939 and 1940 respectively.

Before its entrance into the tongue the hypoglossal nerve divides into one medial nerve and one lateral nerve, the latter consisting of a group of slender branches, most of which are destined to the extrinsic muscles lying immediately dorsally to the nerve. Just before or after the place where the branches

enter the muscles of the tongue a macroscopically well visible anastomosis is established with the lingual nerve. This anastomosis is described in most text-books of anatomy and has recently been emphasized in a work by FITZGERALD and LAW (1958) to be discussed more fully later on. Some centimetre before the place where the nerve begins to split up into its end branches it gives off a branch which runs medially to the geniohyoid muscle.

# MORPHOLOGICAL INVESTIGATIONS

## Introduction

Much work has been devoted to the search for proprioceptive sensory endings in the tongue muscles of different animals. The present work started with a restudy of this problem to get a basis for the following study. By applying different methods, some earlier not used in this very problem, a better knowledge of the morphological background might be gained.

Morphological investigations have been carried out along the following lines and with the following questions:

1) A search for muscle spindles in the extrinsic and intrinsic tongue muscles in the cat.
2) Does a count of the fibres in the hypoglossal nerve proximally and distally reveal any difference in number of fibres that can mean that the nerve receives an addition of fibres from some other nerve?
3) Is there any difference between the calibre spectrum of the hypoglossal nerve proximally and distally which can be of any physiological importance?
4) Are there any differences of physiological importance in the calibre spectras of the different branches of the hypoglossal nerve?
5) Anastomoses between the lingual and hypoglossal nerves. What types of fibres do they contain?
6) Calibre spectras of the lingual and glossopharyngeal nerves.

CHAPTER 1

# Muscle Spindles in the Tongue Muscles

## EARLIER INVESTIGATIONS

The earliest report about the presence or absence of muscle spindles in the human tongue dates from 1894, when FORSTER described them in one of the extrinsic tongue muscles (m. genioglossus). BATTEN (1897) was not able to find spindles in man's tongue nor did he find them in the diaphragm or the ocular muscles. HEWER (1935) working with silver stained embryological material was not able to find any muscle spindles in the tongue muscles. In 1953, however, S. COOPER described muscle spindles in the intrinsic muscles of the human tongue.

Turning to animal material, quite a number of investigations have been carried out. In her above-mentioned study (1953), S. COOPER also reported muscle spindles in the tongue of the rhesus monkey. The first who reported his finding muscle spindles in the intrinsic tongue muscles of lower mammals was LANGWORTHY (1924, b). He used methylene blue and stated that the spindles were easily found in all the species he examined (pig embryos, cats, dogs, opossums and rats). He furthermore reported that the spindles remained unaltered after section of the lingual and glossopharyngeal nerves in the cat, but disappeared after section of the hypoglossal nerve. Out of this he drew the conclusion that the afferent fibres follow the hypoglossal nerve and their central course should according to him be either by the small dorsal root and ganglion that can sometimes be found in connection with the hypoglossal nerve or by the second cervical nerve.

In 1936 (a), TARKHAN reported his findings of muscle spindles in the intrinsic tongue muscles of the rabbit, using silver stain. He also described nerve cells, located along the peripheral course of the hypoglossal nerve. The author was of the opinion that

the afferent fibres from the endings described by him had their perikarya among these cells.

Against the findings of these two authors stand the reports by several other investigators, who have not found any spindles. Among the earliest of these are SHERRINGTON (1894) and BAUM (1900). SHERRINGTON used the cat and BAUM the frog. In 1927, BOEKE came to the same result in different kinds of reptiles (silver staining). More recently CARLETON (1937, rabbit, chameleon and ant-bear, silver staining) BOYD (1937, rabbit, silver and methylene blue staining), BOYD (1941, rabbit, htx-eosin and silver impregnation), WEDDELL, HARPMAN, LAMBLEY and YOUNG (1940, rat and rabbit, methylene blue staining), BARNARD (1940, rabbit, silver staining), COOPER (1953, cat and goat, the method not stated with certainty) and LAW (1954, cat, dog and pig, silver staining) have reported the negative outcome of their studies. In the extrinsic tongue muscles, however, some of the last-mentioned authors (WEDDELL, et al.) demonstrated a few atypical endings (situated in the genioglossal muscle). This has been confirmed by BOYD (1941).

## METHODS

It was regarded as necessary in this work to make as many sections as possible of the tongue and this for several reasons. Firstly, the tongue muscles run in three perpendicular directions. Each one of the muscles has to be examined separately in cross or longitudinal sections. Secondly, it was supposed that the muscle spindles—if present—might be localized in certain regions of the tongue. The end organs of the eye muscles were long undiscovered because they were confined to a restricted region in these muscles (DANIEL 1946). Thus, it cannot be taken for granted that the spindles are disseminated through the whole tongue, which they are for example in the leg muscles investigated by HAGBARTH and WOHLFART (1952).

The principal elements of the muscle spindle are well known. For the morphological identification the following parts seem especially important, namely:

1) The nerve fibres and their mode of termination.
2) The connective tissue capsule.
3) The lymph space.
4) The muscle component.

Owing to the orientation of this sense organ parallel to the extrafusal muscle fibres, it is obvious that transverse sections of the muscle to be investigated are very suitable, because such sections permit the identification of at least the three last-mentioned elements of the spindle without difficulty. Another advantage of this way of sectioning the material is that transverse sections make it possible to follow the spindles in serial sections, by which a check of a structure resembling a spindle is easy. In longitudinal sections, the comparatively small diameter of the muscle spindles renders the identification of them more difficult and sometimes impossible.

The most suitable method for staining the muscle spindles is another point worth consideration. One possibility is to use a silver impregnation method, which if successful gives a very good contrast between the grey to light-brown muscle fibres and the black nerve fibres. The various silver impregnation methods are, however, rather difficult to use and can sometimes be misleading, since even slight over-staining may lead the investigator to mistake connective tissue elements for nerve tissue. Silver impregnation is however very useful when the purpose is merely to demonstrate the nervous components of a sensory ending. In such cases longitudinal sections are preferable.

Among other staining methods used in the investigations of muscle spindles are different routine methods. They have proved to be quite satisfactory, when for instance it has been a question of counting the number of muscle spindles in a given muscle. HAGBARTH and WOHLFART (1952) used Hansen's haematoxylin-van Gieson in their examination of certain leg muscles in the cat. Such methods have also been adopted in the search for spindles in different muscles and have given excellent and reliable results. Transverse sections of the muscles are always used in these cases. Generally it can be said that every staining method which gives a good picture of connective tissue and muscle fibres is suitable, since under these circumstances the three

last-mentioned of the earlier mentioned parts of the muscle spindles are well visible. Of course, it is an advantage if in addition to this the nerve components too are distinctive, but this is difficult to obtain.

There are also other histological methods, which can be used to demonstrate muscle spindles. These are, however, more or less special stainings not so well suited for routine purposes and will not be considered here.

## MATERIAL

The intrinsic and extrinsic muscles have been studied separately. By intrinsic muscles is meant the longitudinal, transversal and vertical muscles confined to the mobile part of the tongue. The extrinsic muscles are the genioglossus, styloglossus and hyoglossus muscles, which take their origin from bone. When the intrinsic muscles were studied, the tongues of the cats were removed as far back as possible in order to obtain all the intrinsic musculature. The tongue was divided into four parts by one incision in the midline, and one incision perpendicular to the former dividing the tongue approximately at the half of its length. For this investigation tongues from 8 cats were used and sectioned for silver impregnation in longitudinal sections of the different muscle parts and (in the case of the other methods) transverse sections of the muscles. The silver stained sections were taken between 25 and 50 microns thick and the other 10–20 microns. In the cases of the thicker silver stained preparations all sections were taken but some of them were excluded for technical reasons. When the sections were thinner, they were not all kept but mostly six at 300–500 microns' interval. Altogether the following number of sections were examined with the different staining methods.

| | |
|---|---|
| 1) Gros-Bielschowsky | 143 sections, |
| 2) Palmgren's silver impregnation | 190 sections, |
| 3) Azan | 531 sections, |
| 4) Weigert-van Gieson | 340 sections. |

Of these four series only those stained with Azan and Weigert-van Gieson were complete, i. e. covered the whole tongue.

When the extrinsic muscles were studied, these muscles were removed in another four animals. The genioglossal muscle, which is difficult to remove completely, was isolated as near its origin from the mandible as possible, and separately fixed, sectioned and stained. The two other extrinsic muscles, i. e. the styloglossal and hyoglossal muscles, have separate origins but common insertion, or more correctly, they run the last part of their extralingual course together. For this reason, they have been removed, fixed and sectioned together. The following number of sections of these muscles have been made:

| | |
|---|---|
| 1) Gros-Bielschowsky | 74 sections, |
| 2) Weigert-van Gieson | 864 sections. |

## RESULTS

Microscopical examination at various magnifications of the sections did not reveal any muscle spindles of the appearance and size that is described for instance by BARKER (1948). No other structures of smaller size resembling muscle spindles were seen. No Golgi tendon organs were found. This result is based mainly upon the analysis of the sections stained with Heidenhain's azan and Weigert-van Gieson. It was soon found that it was difficult to obtain successfully stained silver preparations of whole tongues, which for reasons earlier stated was considered as necessary for the examination to be reliable. Both in the longitudinal silver preparations and the transversely sectioned preparations stained according to Heidenhain or Weigert-van Gieson formations slightly resembling muscle spindles were sometimes seen. Examination of the sections one by one in series however always showed that the formations in question were artifacts. In the silver preparations a small nerve trunk could enter and leave the section within a stretch that corresponded to the length of a muscle spindle. In such cases the absence of the muscle components was the fact by which a mistake could be avoided. Transversely sectioned muscles or nerve fibres could also be confusing, but the serial sections always permitted the details to be examined and moreover revealed the size of the

formation in question, which was always found to be too small for an ordinary muscle spindle.

GAIRNS (1953) made an investigation of sensory nerve endings other than taste buds in the submucous tissue of the human tongue. He was able to show the existence of such endings, resembling those of the Meissner and Krause types. The existence of such endings is beyond doubt and they have been found also in the author's material. No attempt has been made to classify these endings in this study.

## DISCUSSION

Against these findings presented here stand the results reported by LANGWORTHY (1924, b). This author states: "There were always large areas, in which the stain was not oxidized and only here and there was it possible to get a glimpse of the innervation of the muscles. Even with these difficulties it was evident that muscle spindles are quite common in the tongue." In his paper, LANGWORTHY did not describe the size or appearance of the muscle spindles he found.

As regards TARKHANS statement (1936, a) it can be said that his micro-photographs are not convincing. In the end organs shown in his paper only nerve fibres are seen. Neither the muscle fibres, nor the lymph space or connective tissue capsule that makes it possible to classify them as muscle spindles do appear in his micro-photographs.

The outcome of my own investigation is the same as that of the others mentioned in the introduction who did not find any muscle spindles in the tongue. It has not been possible to find one single muscle spindle neither in the intrinsic nor in the extrinsic tongue musculature in any of the sections examined (about 2000). From this negative outcome some points worth consideration viz. the number and the size of the muscle spindles can be made. In such a complicated musculature as that of the tongue, their number ought to be quite high to be of any physiological significance, and therefore the possibility of missing them all can be regarded as small. According to various authors, the total length of the muscle spindles can vary between 750 and

7000 microns (MAXIMOV-BLOOM). This is the size of the spindles found in ordinary limb muscles. It is of course possible that the spindles in such a small-fibred musculature as is that of the tongue are of a smaller size. It is therefore perhaps useful to consider the size of those spindles, which have been found in the eye muscles of man and goat (COOPER, DANIEL and WHITTERIDGE 1955). Here they were found to be about 400 microns long. A comparison between the tongue muscles and the eye muscles from this point of view seems to be justifiable and out of this it can with some certainty be stated that muscle spindles, if present in the tongue, are probably not overlooked.

Another point that must be considered here is the possible existence in the tongue of some other sensory ending with the functions of a stretch receptor. Such endings are known to exist in the eye muscles (DANIEL 1946) as spiral nerve endings. Other variations also exist (COOPER et al. 1955). That atypical endings are found in the tongue is claimed by LAW (1954). In her above-mentioned studies on cat, frog and pig she described an end organ "formed by a coil of axis-cylinder enclosed in an oval or pear-shaped capsule, which appears to be a terminal dilatation of the neurilemma". These end organs are situated with their long-axis parallel to that of the muscle fibres. As judged from the pictures that were published in 1958 (FITZGERALD and LAW) their total length is about 100 microns and their width 10–20 microns. They seem to be of a rather uncomplicated construction and are situated in the connective tissue mainly in the vertical and transverse intrinsic muscle groups. The nerve fibres to these structures degenerated after sectioning the lingual nerve, but remained unaffected by section of the hypoglossal nerve.

The reason why they have not been found either in earlier studies or in the author's material might be that they are rather few and besides this small and therefore easily overlooked. Moreover, silver preparations are with all probability necessary to detect these endings.

As a conclusion can be stated that this investigation has not revealed any muscle spindles either in the extrinsic or the intrinsic tongue muscles of the cat. No other sense organs have been found in these muscles.

CHAPTER 2

# Fibre Count of the Hypoglossal Nerve Proximally and Distally

## MATERIAL AND METHODS

In 5 cats a few mm length of the hypoglossal nerve on one side was removed in two places: Firstly in the hypoglossal canal, where the root fibres of the nerve are united to form one single nerve trunk (the canal was opened with a drill), and secondly just distally to the place where the nerve has crossed the carotid artery but before it has started to give off the branches for the tongue muscles. The nerve was fixed in 1 % osmic acid solution and cut transversely in 5 micron thick preparations. These were magnified about 500 times and micro-photographed. The photographs were put together on a piece of cardboard and the number of fibres was then counted.

In every case a dorsal root was searched for on both sides during the dissection. 10 more cats used for physiological experiments were also dissected for this purpose.

## RESULTS

The result of this count is shown in table 1. Each nerve was counted three times for check and as the greatest difference between the different checks amounted to 10 fibres, one of the results was chosen at random. From the table can be seen that the proximal part of the nerve contains more fibres than the distal in four cases.

*Table 1.* Number of fibres in the hypoglossal nerve proximally and distally.

| Cat nr | Prox. | Dist. |
|---|---|---|
| 4 dx | 4474 | 4419 |
| 5 sin | 5246 | 5209 |
| 6 dx | 5238 | 5270 |
| 15 dx | 4848 | 4690 |
| 94 dx | 4990 | 4755 |

## DISCUSSION

The results just described clearly show that no myelinated fibres are added in the periphery to the part of the hypoglossal nerve which is going to the tongue. In every case was checked that no intraspinal anastomoses entered the hypoglossal canal with the root fibres of the nerve. It is possible that fibres from other nerves come to the hypoglossal nerve just distally to the canal, but these fibres obviously leave the nerve again to reach other destinations (e. g. the ramus descendens). No trace of a dorsal root was ever seen, neither in these cases nor in about 10 others, which have been investigated with special regard to this possibility.

The fact that the proximal part of the nerve contains more fibres than the distal in four cases can be explained by the assumption that some small branches can have left the nerve to pass to one of the extrinsic tongue muscles, which lie just dorsally to the nerve at the place, where the piece of nerve was taken. It can of course also be due to a miscount. In the case (cat 15), where the distal part of the nerve contained more fibres than the proximal, the difference amounted to only 32 fibres. This difference can be explained by the method, which contains a certain amount of error especially with regard to the smaller fibres. In any case, the nerve did not receive so many fibres as would be necessary, if the muscle spindle innervation came to it through some other nerve, for example one of the cervical nerves. The contribution ought then to be 30–40 % of the total amount of fibres (SHERRINGTON 1894). One possibility is of course that such a number of fibres have left the nerve and (an equal number of) proprioceptive fibres have been added to it during its course. In such cases however, the calibre spectrum of the nerve ought to differ proximally and distally. That this is not the case will be shown.

CHAPTER 3

# The Calibre Spectrum of the Hypoglossal Nerve

## EARLIER INVESTIGATIONS

For many years various attempts have been made to correlate size with function in the fibres of different nerve trunks. Much work has been devoted especially to the muscle nerves of the extremities. In these nerves the situation was long complicated by the intricacy of the sense organs in the muscles. Since the physiology of these sense organs is now fairly well known, it has become possible to make a comparison between structure (i. e. fibre size) and function in this case.

The earliest information on the fibre size in the hypoglossal nerve derives from KISS and MIHÁLIK (1928). In their investigation (man and dog, osmium method) the following is stated about the hypoglossal nerve: the nerve is a typical motor one with some very thin fibres, probably sensory in function. In 1940, HÄGGQVIST using the rhesus monkey observed that most of the fibres in the nerve were about 6–7 microns in diameter. The Alzheimer–Mann–Häggqvist method was probably used. In 1944 REXED showed that the hypoglossal nerve in man (Alzheimer–Mann–Häggqvist method) has fibres ranging from 2 to 15 microns with only one definite peak, in the adult material ranging from 7 to 9 microns. With this method the shrinkage amounts to around 30 %, from which follows that the peak actually is somewhat higher placed (10–12 microns). In 1945 HAMMOND and HINSEY found that in the cat the smallest fibres are slightly more than 2 microns in diameter and the biggest about 17 microns. The peak was between 7 and 8 microns. In their investigation the measurements were performed in the microscope and not on photographical reproductions of the nerve. The error in performing the fibre analysis in this way is, however, not small (cf. REXED 1944).

*Table 2.* The calibre spectrum of the hypoglossal nerve

| Animal No. | 1–2μ | 2–3μ | 3–4μ | 4–5μ | 5–6μ | 6–7μ | 7–8μ | 8–9μ | 9–10μ |
|---|---|---|---|---|---|---|---|---|---|
| 4C | | | 1.3 | 10.0 | 17.8 | 25.0 | 21.7 | 12.7 | 6.5 |
| 4P | | | 0.3 | 3.0 | 11.6 | 22.2 | 26.1 | 17.7 | 10.0 |
| 6C | | | 0.6 | 4.9 | 14.0 | 25.3 | 25.3 | 13.6 | 6.9 |
| 6P | | 0.4 | 1.2 | 4.3 | 14.1 | 26.6 | 25.5 | 16.6 | 7.4 |
| 94C | | 0.1 | 2.2 | 10.1 | 20.4 | 25.5 | 22.7 | 11.0 | 4.7 |
| 94P | | 0.1 | 0.9 | 4.9 | 13.7 | 23.8 | 26.6 | 16.3 | 7.3 |
| 98C | | | 1.0 | 7.8 | 11.9 | 25.1 | 23.2 | 15.3 | 7.9 |
| 98P | | 0.3 | 2.5 | 9.5 | 17.3 | 24.6 | 22.8 | 11.6 | 5.9 |
| 134C | | 0.1 | 4.3 | 8.4 | 22.4 | 24.3 | 13.7 | 13.1 | 6.1 |
| 134P | | 0.2 | 0.9 | 4.9 | 8.5 | 18.8 | 26.0 | 13.5 | 14.6 |

## MATERIAL AND METHODS

The methods and technique of fibre analysis have been investigated by REXED (1944), to whom is referred for details. The osmium acid staining of the material gives very little shrinkage, while the Alzheimer–Mann–Häggqvist method, used by some authors, gives a shrinkage of more than 30 %. Thus, to be comparable the numbers given by the different authors have to be corrected with a shrinkage factor depending on the method used. The osmium method has been used throughout this investigation.

Adult cats were used, usually killed with ether. The nerves were removed and placed in 1 % osmic acid solution. After embedding in paraffin, sections were made, not exceeding 5 microns in thickness. The sections were magnified 1000 times and photographed, whereupon the measurement was performed on the photographical copies with the aid of a pair of compasses and a scale. The technique used is that described by REXED (1944).

Sections were made of the following parts of the nerve:

1) The central end of the hypoglossal nerve, i. e. the nerve was removed in the hypoglossal canal in the occipital bone

| 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | 16–17μ | 17–18μ | 18–19μ |
|---|---|---|---|---|---|---|---|---|
| 2.0 | 1.1 | 0.4 | 0.6 | 0.2 | 0.1 | | | |
| 4.3 | 1.9 | 1.5 | 0.8 | 0.3 | 0.1 | 0.3 | | |
| 2.7 | 0.9 | 1.5 | 0.7 | 0.3 | 0.3 | | | |
| 2.2 | 1.1 | 0.4 | 0.2 | 0.1 | | | | |
| 2.3 | 0.6 | 0.2 | | | 0.1 | 0.2 | 0.1 | |
| 3.0 | 1.4 | 0.6 | 0.4 | 0.1 | 0.3 | 0.1 | 0.1 | |
| 3.4 | 2.4 | 0.9 | 0.6 | 0.2 | 0.1 | 0.1 | | |
| 2.6 | 1.2 | 0.3 | 0.3 | 0.2 | 0.5 | 0.1 | 0.1 | |
| 4.8 | 1.3 | 0.8 | 0.4 | 0.3 | 0.1 | | | |
| 6.7 | 3.1 | 1.4 | 0.2 | 0.5 | 0.2 | | | |

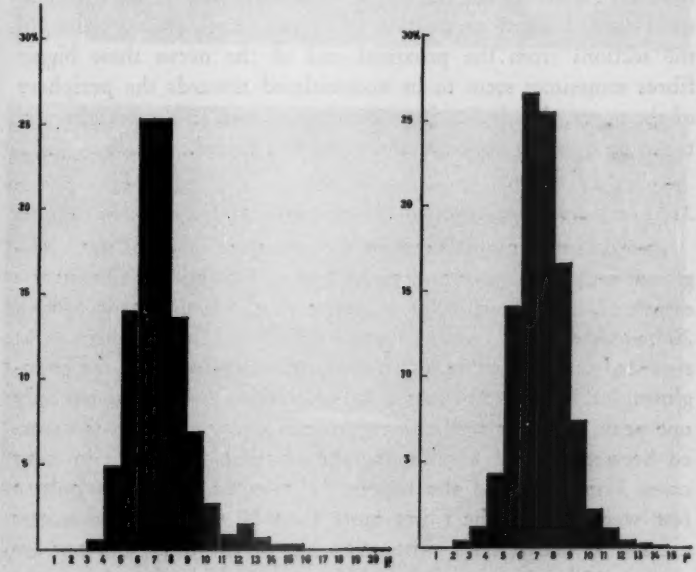


*Fig. 1.* (left) Cat 6. Diagram of calibre spectrum of the hypoglossal nerve, proximal part.
(right) Same nerve, distal part.
In the diagrams the distribution of different fibre sizes is plotted against the percentage of counted fibres in the nerve.

and sections were prepared from the most proximal part possible after the unit of the root filaments.

2) The peripheral part of the nerve distal to the departure of the descendant ramus but proximal to the part where the first branch leaves the nerve.
3) The branch to the geniohyoid muscle.
4) The medial end branch (see ABD-EL-MALEK 1939) supplying mainly the intrinsic musculature.

## RESULTS

### 1) *The distribution of the fibres*

A study of the cross-sections of the nerve proximally and distally revealed a rather uniform distribution of the different fibre types throughout the nerve. Most of the fibres are medium-sized with a small proportion of bigger fibres among them. In the sections from the proximal end of the nerve these bigger fibres sometimes seem to be accumulated towards the periphery of the nerve, thus indicating a common origin. In the peripherally taken sections no such accumulation was found.

### 2) *The calibre spectrum of the nerve proximally and distally*

In 5 different animals calibre spectras were made of the hypoglossal nerve centrally and peripherally. Not all the fibres were measured, but about 1000 in every case, which means around 20 % as the nerve contains about 5000 fibres. This number can be regarded as sufficient in such a uniformly built nerve as the hypoglossal (cf. REXED 1944). As is shown in table 2 the nerve has only one peak, which is well recognizable in every case and is situated between 6 and 8 microns. The smallest fibres are in most cases 3 microns and the biggest 18 microns, of which only a few were found. The fibres more than 10 microns of diameter are not so many, their proportion out of the total sum not exceeding 10 %. No significant difference could be found between the central and peripheral part of the nerve. Fig. 1 shows diagrams of the calibre spectra of the hypoglossal nerve proximally (the nerve was taken out from the hypoglossal canal) and distally

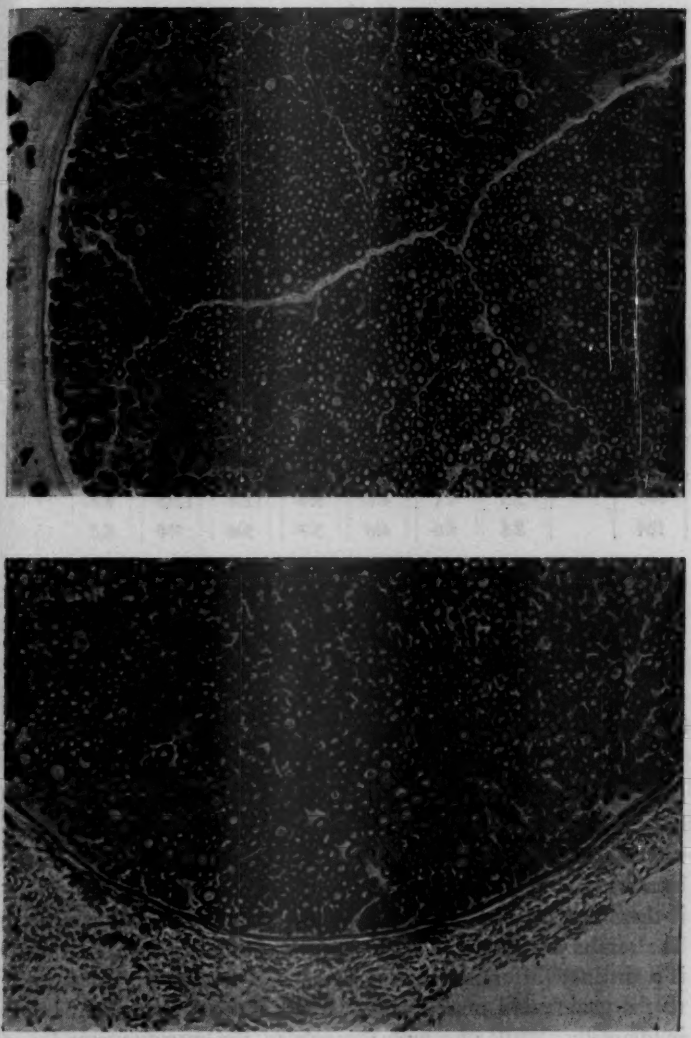


*Fig. 2.* (above) Hypoglossal nerve. Cross section of the proximal part of the nerve. Osmium stain, magnification 190x.
(below) Cross section of the distal part of the same nerve. (Osmium stain, same magnification.)

*Table 3.* The calibre spectrum of the nerve to the intrinsic

| Animal No. | 1–2μ | 2–3μ | 3–4μ | 4–5μ | 5–6μ | 6–7μ | 7–8μ | 8–9μ |
|---|---|---|---|---|---|---|---|---|
| 78 | | 0.3 | 1.7 | 10.7 | 17.4 | 30.0 | 24.4 | 10.7 |
| 79 | | | 0.7 | 3.6 | 10.4 | 30.5 | 36.7 | 13.1 |
| 97 | | | 0.4 | 1.6 | 4.5 | 11.1 | 32.5 | 29.9 |
| 98 | | 0.1 | 1.2 | 5.4 | 15.4 | 31.0 | 26.5 | 13.0 |
| 104 | | | 0.6 | 3.1 | 13.0 | 30.4 | 28.8 | 17.2 |

*Table 4.* The calibre spectrum of the nerve to the geniohyoid

| Animal No. | 1–2μ | 2–3μ | 3–4μ | 4–5μ | 5–6μ | 6–7μ | 7–8μ | 8–9μ | 9–10μ |
|---|---|---|---|---|---|---|---|---|---|
| 78 | | 3.4 | 2.3 | | 2.3 | 4.6 | 8.0 | 12.6 | 8.0 |
| 79 | | 6.6 | 3.3 | 4.4 | 5.5 | 8.8 | 7.7 | 12.1 | 9.9 |
| 98 | | 1.7 | 3.4 | 6.9 | 8.6 | 6.9 | 10.3 | 6.9 | 8.6 |
| 103 | | 3.3 | 4.1 | 4.9 | 5.7 | 11.4 | 12.2 | 9.8 | 11.4 |
| 104 | | 2.8 | 6.5 | 4.6 | 3.7 | 5.6 | 7.4 | 8.3 | 13.9 |

(taken just before the place where the nerve begins to split up into its end-branches). Two cross sections of the nerve are seen in Fig. 2.

3) *The calibre spectrum of different branches of the nerve*

In 5 different animals the branch to the geniohyoid muscle and the branch to the intrinsic musculature (the medial end branch according to ABD-EL-MALEK 1939) were examined. These two branches were chosen as typical examples of extrinsic and intrinsic muscle innervation and could thus be expected to reveal if there are any differences between the fibre sizes in this respect. The results are shown in table 3 and 4. It can be seen that there is a distinct difference between these two branches. The branch to the geniohyoid muscle contains fibres more than 10 microns in diameter, while the main branch to the intrinsic muscles is practically devoid of such fibres. The significance of this will be discussed later (pp. 58, 88). In Fig. 3 a cross section of the branch to the geniohyoid muscle and a diagram of its calibre

muscles

| 9–10μ | 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | 16–17μ | 17–18μ |
|---|---|---|---|---|---|---|---|---|
| 4.5 | 0.5 | | | | | | | |
| 3.6 | 0.7 | | | | | | | |
| 15.0 | 4.7 | 0.3 | | | | | | |
| 6.4 | 1.1 | | | | | | | |
| 5.5 | 0.1 | | | | | | | |

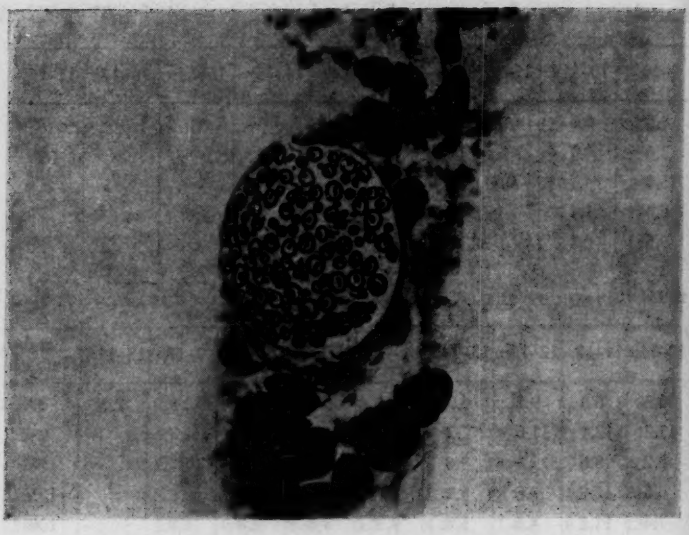
muscle

| 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | 16–17μ | 17–18μ | 18–19μ | Total Number |
|---|---|---|---|---|---|---|---|---|---|
| 10.3 | 6.9 | 9.2 | 6.9 | 3.4 | 5.7 | 11.5 | 2.3 | 2.3 | 87 |
| 13.2 | 12.1 | 11.0 | 2.2 | 3.3 | | | | | 91 |
| 5.2 | 8.6 | 12.1 | 8.6 | 12.1 | | | | | 58 |
| 6.5 | 12.2 | 9.8 | 5.7 | 2.4 | 0.8 | | | | 123 |
| 7.4 | 11.1 | 4.6 | 5.6 | 9.3 | 4.6 | 2.8 | 1.9 | | 108 |

spectrum are shown. For comparison the percentage of fibres in each group is given in the diagram, in spite of the small number of fibres in the nerve. This number can in each case be seen in table 4. In Fig. 4 a diagram of the calibre spectrum of the main branch to the intrinsic muscles and a cross section of this nerve are shown.

## DISCUSSION

In a muscle nerve in the legs the afferent fibres are nearly as many as the efferent ones. Differences exist between extensors and flexors, but the percentage of afferent fibres can be estimated to between 35 and 50 % of the total sum as calculated from the numbers given by REXED and THERMAN in 1948. That the number of afferent fibres is of this order was pointed out already by SHERRINGTON (1894). From the paper by REXED and THERMAN (1948) it is moreover possible to estimate that 35–55 % of these afferents, that is to say around 20 % of the total sum of fibres in the nerve, exceed 10 microns in diameter.



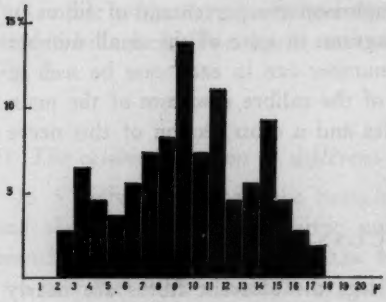
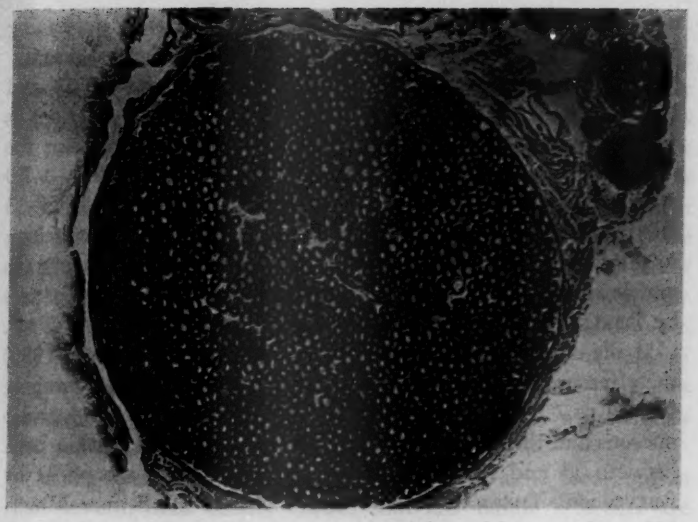



*Fig. 3.* (above) Cat 104. Cross section of the branch to the geniohyoid muscle. (Osmium stain, magnification 190x.)
(left) Diagram of calibre spectrum of the same nerve.

The calibre spectrum of the whole nerve to different muscles in the leg of the cat was worked out by HAGBARTH and WOHLFART (1952). With the use of the osmium method they showed that these nerves have two well-defined peaks in their calibre spectrum. These two peaks belong to two groups of fibres, one ranging from 1 to 9 microns in diameter and the other from 9



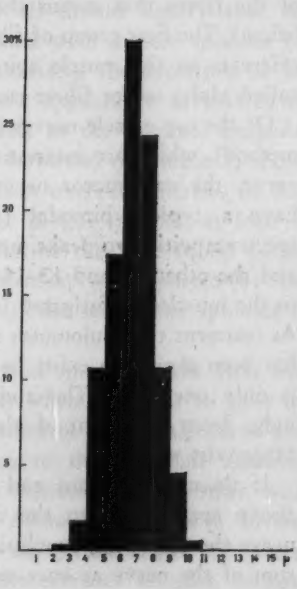



*Fig. 4.* (above) Cat 78. Cross section of the main branch to the intrinsic tongue muscles. (Osmium stain, magnification 190x.)
(right) Diagram of calibre spectrum of the same nerve.

to 19 microns. The peaks are a little unevenly placed, depending on which nerve is investigated, but one of them is usually situated between 4 and 7 microns and the other between 11 and 14 microns in the diagram. If the muscle (tibialis anterior) is de-efferented the afferent fibres turn out to be arranged in the following three groups: 1–5 microns (peak 2–3 microns), 5–10 microns (peak 7–8 microns) and 10–16 microns (peak 11–13 microns). Of these groups the last one has been shown to belong to the fastest afferents (from the so-called nuclear bag) from the muscle spindles. The last figures have been taken from the papers by REXED and THERMAN (1948) and LLOYD and CHANG (1948).

If the nerve is de-afferented (ECCLES and SHERRINGTON 1930) the efferent fibres turn out to consist of two groups: one ranging from 2 to 7 microns in diameter with its peak between 4 and 5 microns and the other ranging from 7 to 17 microns, with a peak between 11 and 13 microns. The values are from the paper by REXED and THERMAN (1948). The modified Alzheimer–Mann–Häggqvist method used in this case is followed by a shrinking of the fibres that means that the actual values are higher (see below). The first group of fibres has been shown to be the gamma efferents to the muscle spindles and the second to be the so-called alpha motor fibres running to the motor end plates.

Of the eye muscle nerves (FERNAND and YOUNG 1951, osmium method), which are interesting to compare with the hypoglossal nerve, the oculomotor nerve in the rabbit has been shown to have a typical bimodal (FERNAND and YOUNG 1951) calibre spectrum with two peaks, one of these situated around 6 microns and the other around 13–14 microns in preparations taken close to the muscles investigated (inferior rectus and inferior oblique). As concerns the oculomotor nerve in man, the same arrangement has been shown to exist. In the trochlear nerve, however, there is only one peak. The abducens nerve in man is difficult to judge from this point of view. (REXED 1944, Alzheimer–Mann–Häggqvist method.)

If these calculations and the facts given in the introduction above are applied to the calibre spectrum of the hypoglossal nerve the following conclusions can be drawn. The whole spectrum of the nerve at once tells us that this nerve is not built in

the same way as are those to the muscles of an extremity. Instead of two peaks it has only one, which is situated where the muscle nerves in general usually have a minimum. From the morphological results it is impossible to state if the afferents or the efferents are dislocated in the spectrum or if one of these groups is missing. One possibility is that the efferents are smaller and that the fibres over 10 microns in diameter, which are between 5 and 15 % of the total number of fibres, are afferent. Another possibility is that all the fibres are efferent and that the single peak of the spectrum is a reflection of the fact that the gamma efferents are missing. A comparison between the spectrum of the hypoglossal nerve and that of certain of the eye muscle nerves and the phrenic nerve (REXED 1944) shows that the motor efferents might well be of the size which forms the peak in the hypoglossal nerve in the cat.

If the spectrum of the hypoglossal nerve, as it turns out in this investigation merely means that the motor efferents are smaller than those of the ordinary muscle nerves and that the bigger fibres are afferents, which all should signify that the intrinsic tongue muscles are furnished with muscle spindles (as is stated by LANGWORTHY and TARKHAN), the spectrum of the whole nerve ought to have the same appearance as that of its branches, especially the main branch to the intrinsic musculature. The spectrum of this branch, however, (see table 3) shows that it is practically devoid of fibres over 10 microns in diameter. This means that the intrinsic tongue muscles, at least in the cat, do not have muscle spindles of the type found in for instance the leg muscles. This statement is supported by the earlier described negative outcome of the search for spindles in these muscles.

The long branch to the geniohyoid muscle is the first one which leaves the hypoglossal nerve, when it begins to split up into its end branches. The examination of this small nerve and the small and very short branches to the different extrinsic muscles shows that they are very similar to each other with regard to their calibre spectrum. Although the nerve to the geniohyoid muscle does not contain more than about 100 fibres, it is taken as a representative of the extrinsic muscles, because

the other extrinsic nerve fibres are not only small but also very short. Besides this it is often difficult to state with certainty if a branch from the hypoglossal nerve is exclusively designated to the extrinsic tongue muscles.

A study of the calibre spectrum of the nerve to the geniohyoid muscle as given in table 4, reveals that it contains many fibres over 10 microns in diameter. Taken as a whole, this spectrum is strikingly similar to that of an ordinary muscle nerve referred to earlier.

A comparison between the spectrum of the hypoglossal nerve proximally and distally shows that the spectrum does not change along the nerve. As earlier shown, counting of the number of fibres proximally and distally showed that no fibres leave or come to the nerve between the hypoglossal canal and the place where the nerve begins to split up into its end branches. These results thus contradict the statement by LANGWORTHY and TARKHAN that the tongue has muscle spindles and that the hypoglossal or cervical nerves are the afferent pathway for the spindles seen by these authors.

It is here appropriate to discuss shortly the findings of sensory type neurones intramedullary, in small dorsal roots or along the course of the hypoglossal nerve. PEARSON found sensory type neurones along the intramedullary course of the nerve in man and made a comparison between these neurones and the mesencephalic nucleus of the trigeminal nerve, thus pointing out their possible proprioceptive nature. It is difficult to tell anything about the function of a nerve cell merely from its morphological appearance, and besides this the number of cells in adult material seems to be far too small for serving the whole proprioceptive function of the tongue. Moreover, the existence of these cells has been questioned by CASASCO (1951). The same can be said about LANGWORTHY's description of the small dorsal ganglia which he found in the cat. Besides this LANGWORTHY (1924 b) states that the root filaments from the dorsal ganglions contain mainly small fibres. If these dorsal roots contained the proposed muscle spindle afferents, much larger fibres (from the nuclear bags, cf. above) ought to be found there. Only once has the present author found a nerve

cell along the extramedullary course of the nerve (this was in a section from the central end of the nerve). That aberrant nerve cells can be found along a nerve is well known and conclusions about their function must be drawn with precaution, especially if their number, as in this case, is small (GRANIT and REXED 1942).

CHAPTER 4

# Connections between the Lingual and the Hypoglossal Nerves

It is now generally accepted that the afferent fibres from the sensory nerve endings in the eye muscles reach the central nervous system via the trigeminal nerve through orbitally situated anastomoses (COOPER, DANIEL and WHITTERIDGE 1955). This is one of the reasons why it seems necessary to consider the lingual nerve, i. e. the trigeminal nerve, as a possible afferent channel also for the proprioception of the tongue. Therefore, a study of the peripheral connections between the hypoglossal and the lingual nerves as well as of the calibre spectrum of the last-mentioned nerve was undertaken in the course of this investigation.

The lingual nerve is the main afferent nerve from the tongue. It carries chiefly two types of fibres from the tongue and they are general somatic afferent and special visceral afferent fibres, the last-mentioned conveying taste and—chiefly at least—later running to the central nervous system via the chorda tympani nerve (cf. COHEN, LANDGREN, STRÖM and ZOTTERMAN 1957). The chorda tympani also contains general visceral fibres designated for the submandibular ganglion, but these fibres do not enter the tongue itself. It is generally considered that the lingual nerve innervates the anterior two-thirds of the tongue, while the same modalities (taste and exteroception) from the posterior third are mediated via the glossopharyngeal nerve.

## EARLIER INVESTIGATIONS

As mentioned in the introductory survey of the literature the existence of peripheral anastomoses between the lingual and hypoglossal nerves in man has long been well known and is

reported in most standard text-books of anatomy (for instance RAUBER–KOPSCH 1955).

A close study of this matter has recently been published by FITZGERALD and LAW (1958). In their investigation, performed on man, dog, cat, rabbit and pig, they made dissections of the nerve trunks in question and were able to show that such connections exist nearly always in the human material and in the whole animal material. In the animals studied the connections in question were found to be situated on the surface of the styloglossus muscle. The anastomoses are established both with the medial and lateral branches of the hypoglossal nerve. The authors could also show that the sensory endings, earlier described by LAW (1954), in the intramuscular connective tissue of the tongue degenerated after section of the lingual nerve and that a partial degeneration of the fibres in the lingual-hypoglossal plexuses occurred after a hypoglossal nerve section. Out of these observations the authors drew the conclusion that the lingual nerve is the proprioceptive pathway from the anterior two-thirds of the tongue.

## OWN OBSERVATIONS

The findings of FITZGERALD and LAW (1958) are confirmed in this work. In the cat anastomoses are regularly found between the lateral and usually also the medial branches of the hypoglossal nerve and the lingual nerve. These communications are peripherally situated and easily damaged during the dissection in the acute experiments. It has therefore not been possible to get good osmium preparations of them to investigate the calibre spectrum with enough accuracy.

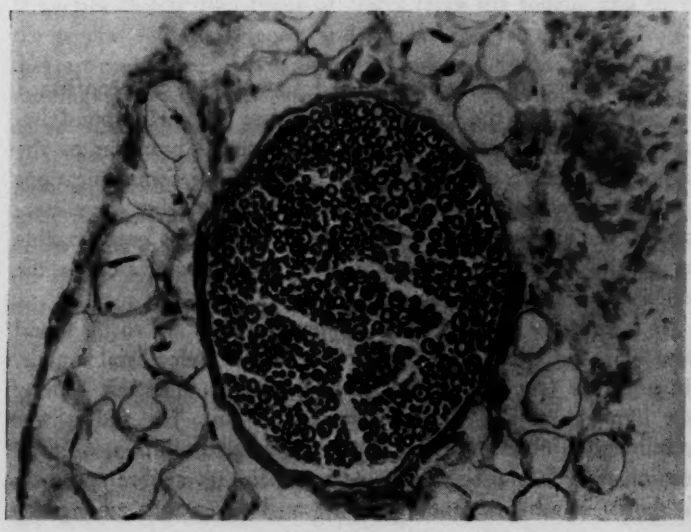
In rare cases however these communications are to be found also more proximally on the surface of the styloglossal muscle. In one case (cat 103, table 5) the branch in question, joining the hypoglossal and lingual nerves, was quite big and it was possible to remove and fix it in 1 % osmic acid solution. A cross-section of this branch is shown in Fig. 5. Its calibre spectrum is shown in table 5. Out of this it can be seen that most of its

*Table 5.* The calibre spectrum of three anastomoses between the

| Animal No. | 1–2μ | 2–3μ | 3–4μ | 4–5μ | 5–6μ | 6–7μ | 7–8μ | 8–9μ |
|---|---|---|---|---|---|---|---|---|
| 97 | 5.5 | 27.2 | 23.6 | 11.9 | 10.1 | 6.2 | 3.0 | 5.0 |
| 98 | 8.0 | 8.0 | 1.1 | 1.2 | 6.9 | 18.4 | 12.6 | 20.7 |
| 103 | 0.1 | 22.4 | 30.9 | 17.5 | 7.2 | 4.3 | 3.0 | 3.8 |

fibres are below 4 microns in diameter (around 53 %), but the rest of them more than that and about 10 % over 9 microns. The biggest fibres were between 13 and 14 microns. The calibre spectra of two other such branches are also shown in the same table. As can be seen their fibre-content is varying. In conformity with the other calibre spectras given here the percentage of fibres has been calculated. If instead absolute numbers had been given it would have been evident that the difference between the nerves with regard to the number of big fibres is not so great.

It is of course impossible to draw any definite conclusions from only three such cases, but it seems reasonable to assume that also the other anastomoses have the same general appearance. In any case, this particular branch does not contain fibres of



| 9–10μ | 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | Total Number of fibres. |
|---|---|---|---|---|---|---|---|
| 4.3 | 2.5 | 0.7 | | | | | 437 |
| 19.5 | 2.3 | | | | | | 87 |
| 4.1 | 3.3 | 1.4 | 1.5 | 0.5 | | | 790 |

the size that are found among the afferents from the muscle spindles in other musculature.

In about ten cats dissections have been made of the hypoglossal nerve proximally to the usual location of the above-mentioned communications with the lingual nerve. It was in these cases constantly found that the fibres which from the medial end branch run medially (chiefly to the genioglossus muscle), contain elements which do not continue centrally or come from the central part of the hypoglossal nerve. These fibres make a loop and turn with the medial end branch in peripheral direction. Their ultimate destination cannot be established with cer-

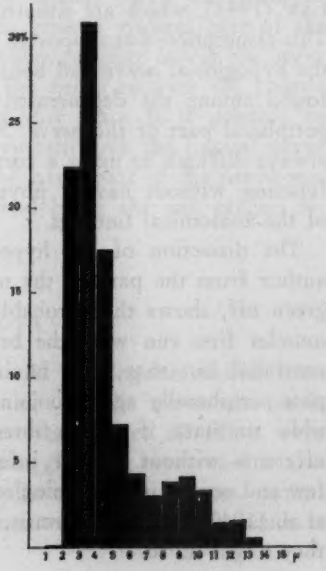



*Fig. 5.* (left) Cat 103. Cross section of an anastomose between the hypoglossal and the lingual nerve. (Osmium stain, magnification 190x.)
(right) Diagram of calibre spectrum of the same nerve.

tainty, but they have to pass over to the lingual nerve more distally as no other nerve communicates with the hypoglossus in this part of its course.

For technical reasons it has not been possible to get well-fixed osmium preparations of these fibres and thus their fibre content cannot be shown. Experiments have been made to try to demonstrate their place of origin by cutting the lingual nerve and make Marchi preparations of the different end branches of the hypoglossal nerve, but the results were (on account of the many pitfalls in this method) not considered as reliable and are therefore not included in this material.

## DISCUSSION

The physiological significance of the connections between the hypoglossal and lingual nerves is difficult to evaluate. FITZGERALD and LAW (1958) are of the opinion that these fibres carry proprioceptive impulses from the endings described by LAW (1954), which are situated in the intrinsic tongue muscles. This assumption was supported by the fact that in animals where the hypoglossal nerve had been divided, intact nerve fibres were found among the degenerated ones to the musculature in the peripheral part of the nerve. Against this can be said that it is always difficult to make a correlation between morphology and function without having physiological experiments in support of the anatomical findings.

The dissection of the hypoglossal nerve performed by the author from the part of the nerve where its first branches are given off, shows that probably some fibres from the extrinsic muscles first run with the branches of the hypoglossal nerve centrally, but that after having reached the main trunk they pass peripherally again to join the lingual nerve. It is not possible to state if these fibres are visceral or general somatic afferents without further information. If the fibres from the few end organs in the genioglossal muscle described by WEDDELL et al. (1940) run with them is of course not possible to say, but they might do so.

CHAPTER 5

# The Calibre Spectrum of the Lingual Nerve

## EARLIER INVESTIGATIONS

The only information about the fibre sizes of the lingual nerve known to the author is given by ZOTTERMAN (1936). In his paper ZOTTERMAN stated that the largest fibres (Alzheimer–Mann method) were 10 microns in diameter. Through physiological experiments he was able to show that these fibres convey touch from the tongue and that the cold fibres investigated at the same time had a fibre size of about 3 microns.

## METHODS AND MATERIAL

Five adult cats were used. The lingual nerve was removed proximally to the point where the general visceral part of the nerve designated to the submandibular ganglion leaves the nerve and distally to the point where the nerve receives the chorda tympani. In sections taken from this place it is possible to distinguish between the chorda tympani and the lingual nerve proper in the microscope. Only the latter part of the nerve was measured in every case, the method being the one earlier described.

## RESULTS

The result is shown in table 6. As nothing has earlier been known about the exact fibre content of the nerve and as it was expected to contain many small fibres all fibres were measured. Thus the number of fibres given in every case is also the total number of myelinated fibres found. A cross section of the lingual nerve and a diagram of its calibre spectrum is shown in Fig. 6.

*Table 6.* The calibre spectrum of the lingual nerve

| Animal No. | 1–2μ | 2–3μ | 3–4μ | 4–5μ | 5–6μ | 6–7μ | 7–8μ | 8–9μ | 9–10μ |
|---|---|---|---|---|---|---|---|---|---|
| 63 | 0.1 | 12.3 | 15.2 | 13.2 | 10.2 | 9.7 | 9.0 | 7.1 | 6.7 |
| 64 | 1.4 | 10.2 | 12.9 | 15.0 | 12.0 | 13.8 | 11.3 | 8.8 | 6.8 |
| 62 | 1.0 | 7.4 | 15.4 | 13.8 | 12.6 | 11.3 | 9.0 | 6.6 | 6.7 |
| 78 | 1.0 | 8.5 | 11.4 | 15.0 | 12.6 | 12.3 | 10.1 | 6.4 | 6.9 |
| 69 | 1.4 | 15.7 | 14.0 | 14.1 | 13.3 | 12.7 | 9.8 | 6.4 | 6.2 |

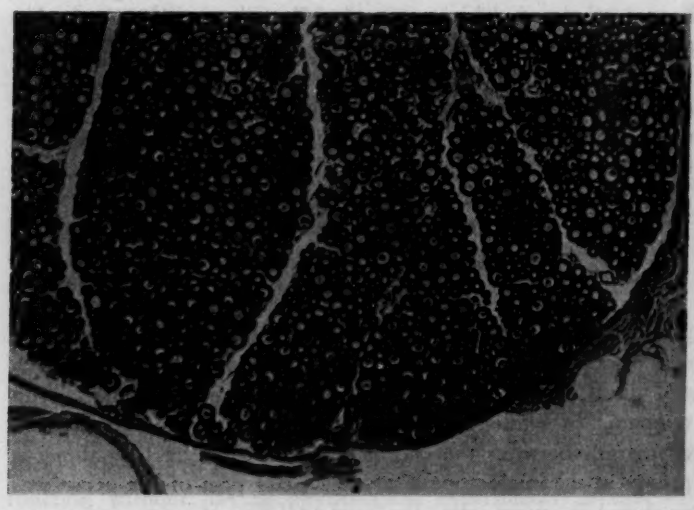


*Fig. 6.* (above) Cat 62. Cross section of the lingual nerve. (Osmium stain, magnification 190x.)
(right) Diagram of calibre spectrum of the same nerve.

| 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | 16–17μ | 17–18μ | Total Number |
|---|---|---|---|---|---|---|---|---|
| 8.0 | 4.4 | 2.8 | 0.9 | 0.1 | | | | 2290 |
| 5.0 | 1.9 | 0.8 | 0.1 | | | | | 2215 |
| 7.5 | 5.6 | 2.4 | 0.6 | 0.2 | | | | 2275 |
| 7.4 | 4.8 | 2.5 | 0.8 | | | | | 2002 |
| 3.7 | 1.8 | 0.8 | 0.1 | | | | | 2405 |

## DISCUSSION

No more than the hypoglossal nerve the lingual nerve has fibres of the large size, which is found among the afferent fibres from muscle spindles. That the autonomic fibre content in this nerve is high is evident. The fact that so few fibres between 1 and 3 microns in diameter are found is probably due to the difficulties in staining and measuring such small fibres. However, more than 50 % of the myelinated fibres in the nerve are more than 5 microns thick. Among these are touch and cold fibres as well as other fibres from the mucous parts of the tongue (ZOTTERMAN 1936). The slight difference with regard to the maximum fibre diameter between the author's material and that of Zotterman is comprehensible out of the different methods used. Zotterman found no fibres exceeding 10 microns in diameter, but he used the Alzheimer–Mann method, which as mentioned before causes a shrinkage of about 35 %. If among the larger fibres there are any serving proprioceptive functions is at this point of the investigation impossible to state. As no reliable information exists about the number of different receptors in the tongue of the cat, no estimations can be made of what number of fibres is required for different modalities. As a consequence of this it cannot be stated if there are any fibres left for any proprioceptive nerve endings. Such calculations have been made in the case of muscle nerves and spindles in the extremities (see GRANIT 1955).

CHAPTER 6

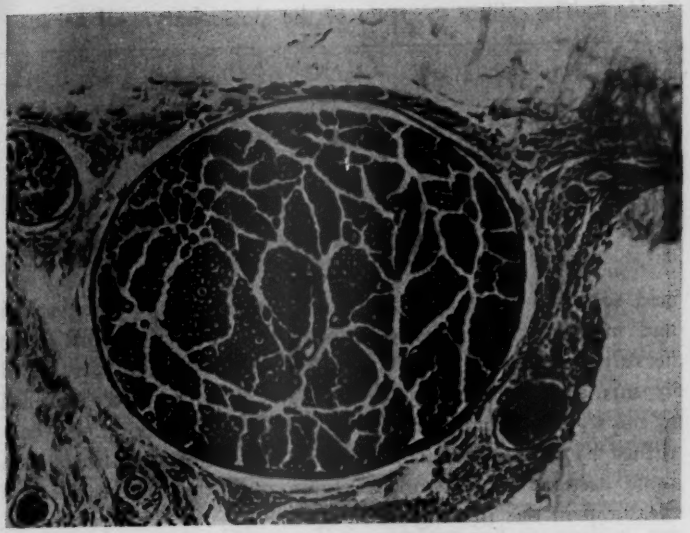
# The Calibre Spectrum of the Glossopharyngeal Nerve

The first branch given off from this nerve during its extracranial course is the tympanic nerve, innervating the parotid gland. The rest of the fibres are distributed to the carotic sinus region, the pharynx muscles, the stylopharyngeus muscle, the tonsillar region and the posterior third of the tongue. That there are both special afferent fibres (taste) and general afferent fibres (touch etc.) among the last-mentioned fibres in the nerve was shown by ZOTTERMAN (1935). Thus the nerve can be said to be equivalent to the lingual nerve but for the posterior part of the tongue. For this reason it seemed necessary to make an investigation of the size of the fibres in that part of the glossopharyngeal nerve, which innervates the tongue.

It has not been possible to get detailed information on the calibre spectrum of the glossopharyngeal nerve from the literature. ZOTTERMAN (1935) stated that "a fairly great number of large fibres up to 13 microns are seen among the mass of small fibres". The osmium method was used. HÄGGQVIST in his review of the motor nerves (1940) remarked that there are both thicker and thinner fibres in the nerve.

## MATERIAL AND METHODS

Five adult cats were used. The nerve was identified at the place where it crosses the bulla mastoidea and isolated just before passing the stylopharyngeus muscle, where it begins to split up into its end branches. In this place the nerve was removed, which means that the sections prepared contained the branches to this muscle, those to the tonsillar region and the lingual branch, but not the sinus nerve. The material was fixed in 1 % osmic



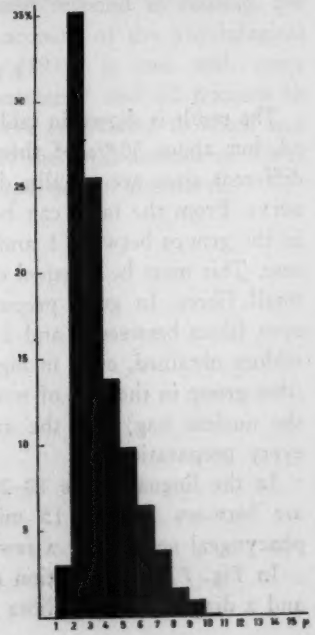



*Fig. 7.* (above) Cat 117. Cross section of the glossopharyngeal nerve, lingual branch. (Osmium stain, magnification 190x.) (right) Diagram of calibre spectrum of the same nerve.

*Table 7.* The calibre spectrum of the glossopharyngeal nerve

| Animal No. | 1-2μ | 2-3μ | 3-4μ | 4-5μ | 5-6μ | 6-7μ | 7-8μ | 8-9μ | 9-10μ |
|---|---|---|---|---|---|---|---|---|---|
| LS 10 | 0.7 | 12.7 | 31.2 | 27.2 | 12.9 | 9.3 | 3.8 | 1.7 | 0.3 |
| 115 | 0.7 | 37.5 | 29.1 | 16.0 | 7.2 | 5.1 | 2.1 | 1.6 | 0.5 |
| 116 | 0.5 | 29.8 | 31.5 | 16.5 | 9.8 | 6.7 | 2.3 | 2.1 | 0.3 |
| 117 | 3.0 | 35.2 | 25.5 | 13.8 | 9.8 | 6.4 | 3.8 | 1.6 | 0.9 |
| 118 | 10.0 | 44.5 | 21.5 | 10.4 | 6.3 | 4.5 | 1.6 | 0.9 | 0.2 |

acid solution, cut into sections 5 microns thick, photographed and measured as earlier described. In the sections one large nerve trunk containing about 2000 fibres was found surrounded by smaller branches. That these smaller branches were destined to the stylopharyngeus muscle and the tonsillar region was confirmed by macrodissection. In order to get no other fibres than those destined to the tongue region only the big branch was measured in this investigation.

## RESULTS

The result is shown in table 7. Not all the fibres were measured, but about 50 % of them chosen at random. The fibres of different sizes are equally distributed in a cross section of the nerve. From the table can be seen that the proportion of fibres in the groups between 1 and 4 microns is varying from case to case. This must be a sequel of the difficulties in measuring such small fibres. In good preparations it was possible to identify even fibres between 1 and 2 microns, but such preparations are seldom obtained, even in big materials. Anyhow, the important fibre group in the case of stretch receptors is the large one (from the nuclear bag) and the amount of coarse fibres is equal in every preparation.

In the lingual nerve 10–20 % of the total amount of fibres are between 10 and 15 microns in diameter. In the glossopharyngeal nerve only a few fibres of this size are found.

In Fig. 7 a cross section of the lingual branch of the nerve and a diagram of its calibre spectrum are shown.

| 10–11μ | 11–12μ | 12–13μ | 13–14μ | 14–15μ | 15–16μ | 16–17μ | 17–18μ | 18–19μ |
|---|---|---|---|---|---|---|---|---|
| 0.1 | 0.1 | | | | | | | |
| | 0.1 | | | | | | | |
| 0.3 | | | | | | | | |
| 0.1 | | | | | | | | |

## DISCUSSION

The glossopharyngeal nerve does not have fibres that can be the nuclear bag afferents form the muscle spindles. In contrast to the spectrum of the lingual nerve that of the glossopharyngeal one shows very few fibres more than 10 microns in diameter. In the lingual nerve these bigger fibres are, according to HENSEL and ZOTTERMAN (1951), exclusively touch fibres, whereas the touch and pressure fibres, which also respond to cooling, are smaller, around 8–10 microns. On account of the physiological findings reported by ZOTTERMAN (1935) it can with some certainty be said that the fibres between 7 and 10 microns in diameter in the glossopharyngeal nerve are related to touch and pressure. They do not exceed 5 % of the total amount of fibres and must be regarded as a small proportion of the nerve.

# General Comments and Conclusions on the Morphological Findings

The function of the system of which muscle spindles are part, is now fairly well known. The proprioceptive system of the limb muscles is a very elaborate mechanism, which can be regarded from a qualitative as well as a quantitative point of view with regard to the morphology of the specific sense organ, its afferent and efferent paths and their central organization.

Nothing contradicts the hypothesis that such a system, if present in the tongue, should exhibit the same general characteristics with regard to the relative number of muscle spindles, the size of the afferent and efferent nerve fibres etc. as that in the muscles of the limbs. The complex arrangement of the tongue muscles even makes it probable that the system ought to be very well developed and consequently easily demonstrable histologically.

The results of the morphological part of the investigation can be summarized as follows:

1) No muscle spindles have been found in the extrinsic or intrinsic tongue muscles of the cat.

2) The fibre count of the hypoglossal nerve has shown that with all probability no fibres destined to the tongue are added to the hypoglossal nerve during its course from the hypoglossal canal to the place where the terminal ramification of the nerve starts.

3) Neither the hypoglossal, nor the lingual nor the glossopharyngeal nerve contains fibres that can be nuclear bag afferents from muscle spindles.

4) In conformity with the findings of FitzGerald and Law (1958) the hypoglossal nerve has been found to anastomose with the lingual nerve. From the available morphological data nothing can be said about the function of these anastomoses.

The morphological findings clearly point to the absence of a proprioceptive system with muscle spindles as the receptor organs in the tongue muscles of the cat. It is however highly probable that the nucleus of the hypoglossal nerve is influenced by other afferent systems. An especially interesting question is if there are any other afferent mechanisms located in the tongue itself that are capable of influencing its movements. To get further information about this and other possible afferent channels physiological methods have been used.

# PHYSIOLOGICAL INVESTIGATIONS

## Introduction

The attempts to attack the problem of proprioception in the tongue with physiological methods have been few compared with the number of morphological studies in the field. Several of the investigators have used dilatation of the pupil and a rise in the arterial blood-pressure after stimulation of the central end of the cut hypoglossal nerve as indications of the presence of proprioceptive afferents in the nerve. WEDDELL, HARPMAN, LAMBLEY and YOUNG (1940) noticed these reactions, which however were abolished when anastomoses between the hypoglossal nerve and the superior cervical ganglion were destroyed. From this they concluded that the reaction in question was an autonomic reflex.

The first to describe action potentials in the afferent tongue nerves in response to touch was ZOTTERMAN (1935), who recorded such potentials in the chorda tympani and glossopharyngeal nerves.

BARRON (1936) tried to obtain afferent impulses in the hypoglossal nerve of cats, rabbits and rats, in response to stretch, evidently on the assumption that muscle spindles—as described by LANGWORTHY (1924 b)—should be present in the tongue. He did not, however, obtain any afferent activity in the hypoglossal nerve, whereas it could be recorded in the lingual nerve.

The same year TARKHAN (1936 b) reported a series of experiments on cats and dogs, in which he stimulated the central end of the cut hypoglossal nerve. He found a rise in blood-pressure in response to stimulation of the hypoglossal nerve and considered that as proof of the existence of afferent proprioceptive fibres in the nerve. Reflex movements of the tongue were recorded on a kymograph, when the central end of the cut medial hypoglossal end branch was stimulated with the rest of

the innervation preserved. This result will be discussed in the chapter dealing with recurrent inhibition. In another report (1936 a) TARKHAN reported that muscle spindles are present in the tongue muscles and that sensory cells were scattered along the peripheral course of the nerve. From these two findings Tarkhan concluded that the hypoglossal nerve is a sensori-motor one.

Using the cat DOWNMAN (1939) performed experiments of the same type as TARKHAN and he also considered dilatation of the pupil and a rise in arterial blood-pressure as a proof of the existence of afferents in the hypoglossal nerve. He found that the afferents from the tongue pass via the hypoglossal nerve and enter the central nervous system either with the hypoglossal nerve or by way of the vagus or the accessory nerves. DOWNMAN did not obtain any effects when the tongue was stimulated directly in different ways (after division of the lingual and glossopharyngeal nerves) and considered this to be due to inadequate stimulation of the nerve endings. As the effects obtained were not abolished by section of the dorsal roots of the two upper cervical nerves, DOWNMAN concluded that these nerves do not take part in the innervation of the tongue.

CORBIN and HARRISON (1938) reported a negative outcome of their attempts to record afferent impulses in the hypoglossal and lingual nerve or upper cervical roots when stretching the tongue in cats. With regard to the lingual nerve the authors stated that the intense activity in response to touch made definite conclusions difficult.

TARKHAN and ABOU-EL-NAGA made a new study of the problem in 1947. They found that mechanical and electrical stimulation of the central end of the divided hypoglossal nerve caused a rise in blood-pressure of dogs both in normal animals and in animals where the rootlets of the hypoglossal nerve had been destroyed. They also found that root sections of the cervical nerves did not cause any degeneration in the hypoglossal nerve, which however was the case when the ganglion nodosum was removed. From this the authors claimed that the afferent fibres from the muscle spindles in the tongue, described by TARKHAN

(1936 a cf. page 16) enter the brain stem chiefly via the vagus nerve.

COOPER (1954) was the first to report impulses influenced by stretch of the tongue in filaments of the medial end branch of the hypoglossal nerve in the cat. In contrast to the authors earlier mentioned, COOPER in an earlier work (1953) had not found muscle spindles in the intrinsic tongue muscles of the cat. She regarded the physiological results as "a proof that peripheral fibres of the hypoglossal nerve carry afferent discharge during stretch of the tongue".

As is seen from these reports, the results and opinions are divergent. In this part of the study the following problems have been treated:

1) Is there any sign of afferent activity in the tongue nerves that can be evoked by stretch or contraction of the tongue muscles?
2) Can any reflex pathways be activated with any of the tongue nerves as afferent arc and the hypoglossal nerve as efferent arc?
3) How are the hypoglossal motoneurones arranged with respect to recurrent inhibition?
4) What functional connections exist between the jaw muscles and the tongue muscles?

CHAPTER 7

# Afferent Activity in the Tongue Nerves

As earlier mentioned, COOPER (1954) recorded afferent impulses in the hypoglossal nerve of the cat. These impulses were obtained in filaments from the main branch to the intrinsic muscles "isolated under the jaw near the entry to the muscles". Some of the impulses were influenced by stretch of the tongue. These findings at the first glance seem to be a positive proof of the view that the whole hypoglossal nerve is a sensori-motor nerve. However, as was also emphasized by COOPER, they only mean that afferent fibres are present in the most distal part of the nerve, close to its entrance into the tongue. What way the fibres in question take to the central nervous system is still an open question. As a matter of fact, they might well turn away from the hypoglossal nerve via the earlier mentioned connections between this nerve and the lingual nerve.

Turning to fibres conveying touch and pressure from the tongue it has long been well known that they reach the central nervous system by different routes, i. e. in the lingual and glossopharyngeal nerves. It has been suggested that the chorda tympani nerve also contains touch fibres. This was also found in the experiments by COHEN, LANDGREN, STRÖM and ZOTTERMAN (1957), in which they showed that single cortical cells are fired by touch impulses from the tongue passing in the chorda tympani nerve. Furthermore they showed that the cortical sensory areas for the lingual and chorda tympani nerves overlapped each other. From the posterior third of the tongue the general somatic afferent fibres reach the central nervous system by way of the glossopharyngeal nerve, which was first shown by ZOTTERMAN (1935). LANDGREN (1957), when studying the discharge in cortical cells after varying stimulation of the tongue, observed cortical cells discharging after stretch of the tongue.

In this case however: "stretch stands for a group of different stimuli assumed to affect stretch receptors in the tongue and (or) masticatory muscles. The stimuli were: stretching the tongue, tongue movements, pressure on the tongue, swallowing and movements of the lower jaw."

From the above-mentioned experiments can be concluded that the general afferent fibres from the anterior two thirds of the tongue are shared between the lingual (trigeminal) and chorda tympani (facial) nerves and that they are not reserved for the lingual nerve alone, which was earlier generally accepted.

## METHODS AND MATERIAL

Twenty-five cats were used. The anaesthesia was started with ether followed by Nembutal 40 mg/kg body weight intraperitoneally. A tracheal cannula was inserted. The skin was incised in the midline in the submandibular region and the mylohyoid muscle divided. Depending upon what nerve was to be used the dissection was completed as follows:

The hypoglossal nerve was dissected free from where it crosses the carotid artery up to its entrance into the tongue. It was divided near the carotid artery and filaments were dissected out from the peripheral part of the nerve.

The lingual nerve on one side was exposed after a resection of the mandible. The nerve was cut distally to its junction with the chorda tympani nerve. Filaments were isolated from the distal part of the nerve.

The glossopharyngeal nerve was isolated just medially to the bulla mastoidea and followed peripherally as long as possible, cut and similarly dissected into fine filaments.

The tongue was stretched in the following two ways. In some experiments a thread was attached to the tip of the tongue, by which it was stretched, carefully avoiding to touch the surrounding tissues. This was rather easily accomplished in the experiments where the mandible was removed. In other experiments the tongue was moderately stretched by two threads from the base of the tongue running obliquely backwards and

attached to the experimental table and further by a thread through the tip of the tongue running forwards to a myograph, by which changes in tension thus could be recorded. The hypoglossal nerve was stimulated and the activity in the lingual nerve recorded during the muscle-twitch set up in response to the stimulation.

The blood-vessels to the mouth region were preserved as much as possible during the dissection. None of the main arteries was interfered with. In the experiments where the mandible was removed the mandibular artery had to be ligated.

The isolated nerve filaments were kept in a paraffin pool at 37° C. The action potentials were led off with silver electrodes and fed to a push-pull amplifier through a cathode follower input. The impulses were made visible on a double beam cathode ray tube and made audible by a loud-speaker. Records were made on continuously running bromide paper.

## RESULTS

### 1. *The hypoglossal nerve*

When the main hypoglossal trunk was dissected and filaments from this part of the nerve (before the first branches are given off) were put on the electrode impulses were never obtained when the tongue was stretched.

When the dissection was made more peripherally, at the place where the nerve is split up into its branches, action potentials could sometimes be recorded from certain filaments in the distal part of the divided hypoglossal nerve in response to stretch. The impulses so obtained were observed in the medial end branch supplying the intrinsic tongue muscles. Sometimes the filament giving the impulses was situated close to the mentioned end branch, sometimes it was incorporated with this. It is possible that the branches in question come from the genioglossal muscle near its origin, since the muscle fibres composing this muscle begin to radiate into the tongue almost immediately after their origin from the inner surface of the mandible bone. Therefore,

the nerve fibres to this part of the genioglossal muscle follow the main hypoglossal trunk to reach their destination. It is however not possible to localize exactly in which muscle the afferent fibres in question originate. That they might come from the end organs in the genioglossal muscle described by WEDDELL et al. (1940) is suggested by the fact that these afferent impulses were never obtained in the experiments where the mandible was removed, in which case the origin of the muscle is removed. This can have the effect that the end organs in question are damaged, as they are situated in this part of the muscle, or that the tension in the muscle has decreased so much that they do not fire in response to stretch.

Afferent impulses were never recorded from nerve fibres, which could with certainty be traced to any of the extrinsic tongue muscles. As was mentioned in the chapter dealing with the calibre spectrum of the different branches from the hypoglossal nerve, the branch to the geniohyoid muscle was found to contain comparatively many fibres more than 10 microns in diameter. The spectrum is in fact very like that of a nerve to a muscle furnished with muscle spindles. Repeated experiments have never revealed any afferent activity in the nerve to this muscle neither during stretch of the tongue or movements of mandible, nor through direct pressure upon the muscle or stretch applied to the muscle itself.

### 2. *The lingual nerve*

Many lingual nerve fibres were isolated and recorded from. That the fibres tested were alive was checked by a stroke over the surface of the tongue. This stimulation always gives activity in the lingual nerve and most of its filaments.

Large spikes in response to touch were easily obtained in isolated filaments of the lingual nerve as described by ZOTTERMAN (1936). It was also possible to find fibres responding to pressure on the surface of the tongue. However, the author never succeeded in finding fibres with activity induced by stretch, performed by pulling the tongue out of the mouth.

In the experiments where the mandible was removed and

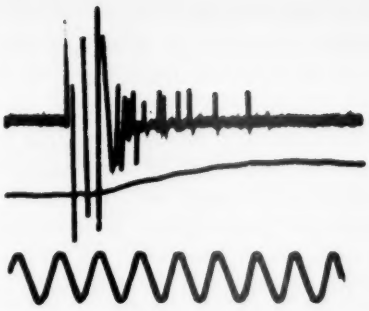


*Fig. 8.* Afferent discharge in a filament from the lingual nerve in response to a shock applied to the hypoglossal nerve. The contraction of the tongue is indicated by signal line. Time 100 cy/sec.

the tongue of the animal was fixed in a slightly stretched position as described above (cf. page 56) activity in fibres of the lingual nerve was recorded, when the hypoglossal nerve was stimulated with a single shock producing a contraction of the tongue. As is seen from Fig. 8, the end organs giving rise to these spikes were silent before the shock was applied to the hypoglossal nerve with the tongue slightly stretched. Their relation to the contraction is shown in the same Fig. The findings described returned in every experiment performed in this way. If the sense organs are rapidly adapting or not cannot be stated as the stimulus, contraction, is not maintained. The experimental situation is similar to that in which activity is recorded in a dorsal root in response to stimulation of the peripheral end of a cut ventral root with a shock maximal for the alpha fibre. In such a case one early, ephaptic spike can be recorded, followed by an early discharge set up by the stimulation of the sense organ by the alpha fibres (cf. GRANIT, POMPEIANO and WALTMAN 1959). If the muscle was tetanized in order to get a maintained contraction to study the adaption process of the sense organ, a series of ephaptic spikes might be set up interfering with the results.

3. *The glossopharyngeal nerve*

In these experiments the results were the same as with the lingual nerve. However, touch responses in this nerve are by no means so easily obtained as in the lingual nerve. This might be due to the following facts. Firstly, compared with the lingual nerve, thick fibres are rather few in the glossopharyngeal nerve, which is also practically devoid of fibres over 10 microns in diameter (cf. table 7). These fibres, as shown by ZOTTERMAN, are those conveying touch. Secondly: on account of its deep localization the glossopharyngeal nerve is easily damaged during the dissection.

## DISCUSSION

The results described here confirm COOPER's finding (1954) of afferent impulses in the hypoglossal nerve. The impulses observed were obtained only from what can be called the end-branches of the nerve near the tongue muscles. They seem to be confined to branches from the intrinsic musculature or to branches which pass through this. Although no definite evidence can be put forward, much points to the genioglossal muscle as the localization of the end organs producing this response. This is interesting because end organs in this muscle have been described by WEDDELL et al. (1940). However, attention must in this connection be paid also to the end organs described by LAW (1954), LAW and FITZGERALD (1959). As a general statement can be said that the fibres leading afferent impulses in the hypoglossal nerve are few in number and not easily found, which might be the explanation of earlier failures to find them. Another explanation might be that they have been searched for too proximally in the nerve.

That fibres leading afferent activity have never been found in the main hypoglossal nerve trunk might have two reasons. The fibres might be so few in number that they are lost during the dissection. This could mean that there were in fact afferent fibres going to the central nervous system by way of the hypoglossal nerve. This possibility can however to some extent be tested with other neurophysiological methods.

Another reason for the missing afferents in the main hypoglossal nerve trunk might be that the fibres found in the periphery leave the hypoglossal nerve and turn to the lingual nerve by way of the anastomoses earlier described. Since only afferent somatic fibres are known in the lingual nerve, it seems justified to regard the components in these anastomoses as afferent. The calibre spectrum of these anastomoses (table 5) showed that they contain a certain proportion of big fibres, which might be the afferents in question. (In this discussion the autonomic components are not considered.) Attempts to record from these peripheral connections have, however, never been successful, probably because the fibres are very easily destroyed during the dissection.

The experiments have shown that the sense organs can be fired by applying a stimulus to the hypoglossal nerve causing a contraction of the tongue muscles. From this follows that the end organs like the Golgi tendon organ must be situated in series with the muscle fibres, otherwise they could not be stimulated by the contraction. If they are situated in series with the muscle fibres it must hovewer also be possible to stimulate them by a passive stretch of the fibres. When the tongue was pulled out of the mouth, no response could however be recorded. This can be due to two factors: either the wrong muscles are pulled or the pull has not been fast enough compared with the contraction, or both factors. However it also means that a rapid stretch such as the one set up by an active contraction might be the right way of evoking activity from these end organs. The sense organs firing at touch, pressure and pinch of the tongue are rapidly adapting. Moreover they are situated in series with the muscle fibres which insert at the submucosal border. Thus it is probable that the end organs stimulated by an active contraction of the tongue muscles are identical with the rapidly adapting touch, pinch and pressure organs situated in the submucosal part of the tongue. That could explain why there is no response to the slow passive stretch of the tongue. One possible exception from such a way of activation is the afferent activity in the hypoglossal nerve originally observed by COOPER (1954) and confirmed in this investigation.

It has been demonstrated here that the lingual nerve is the main somatic afferent channel from the tongue. The next step is to study the reflex activity that can be set up from these afferent channels recording it either in the hypoglossal nerve or the tongue. In such experiments the relative importance of the different nerves can be studied with regard to their influence on tongue muscle activity.

## SUMMARY

Results have been presented showing that fibres with activity produced by stretch of the tongue are present in the hypoglossal nerve in its most distal part just before and at its entrance into the tongue, but also that this activity could not be obtained in the main trunk of the hypoglossal nerve. It has further been shown that besides touch and pressure also a contraction of the tongue evokes activity in the lingual nerve. The mechanism by which this activity is evoked has been shortly discussed.

CHAPTER 8

# Reflex Activity in the Hypoglossal Nerve and the Tongue Muscles

TARKHAN (1936 b) reported reflex movements of the tongue after stimulation of the lingual and hypoglossal nerves in dogs and cats. After partial division of the hypoglossal nerves TARKHAN stimulated the central ends of the nerves mechanically (by pinching) and recorded movements of the tongue by connecting the tip of the tongue with a kymograph by a thread. The movements registered in this way were taken as a proof of the existence of a crossed reflex path between the lingual and the hypoglossal nerves and a reflex path also in the hypoglossal nerves. That the reflex in the hypoglossal nerve also is uncrossed was suggested by the results of other experiments, in which a reflex movement of the tongue was obtained, when one hypoglossal nerve was cut and also the medial part of the other, which was then stimulated mechanically at its central end. The reflex movement obtained could only be mediated through the intact innervation on the same side. TARKHAN's conclusion was that the supposed afferents in the hypoglossal nerve are probably proprioceptive, but that also the lingual nerve has central connections with the hypoglossal nucleus, through which movements of the tongue can be elicited.

In the course of their studies on the jaw and tongue movements SCHOEN (1931), SCHOEN and KOEPPEN (1931) evidently did not get such a reflex contraction when stretching the tongue in thalamic cats, but on the other hand observed tongue movements as the result of touch, pinch and other ways of handling the tongue.

## METHODS AND MATERIAL

Altogether 73 cats were used in these experiments. The method used for dissecting and performing the experiments was the following in the different types of experiments:

1. In one series of experiments 10 full-grown cats were used, five of which were decerebrated intercollicularly and the others anaesthetized with Nembutal (40 mg/kg body weight) or chloralose (60 mg/kg body weight). The skin was incised in the midline and the hypoglossal nerve exposed by division of the mylohyoid muscle. The different end branches of the hypoglossal nerve were dissected free and cut as distally as possible to obtain a proper length of nerve for stimulation and recording. The lingual nerves were cut. In some experiments the glossopharyngeal nerves and the facial nerves extracranially and the trigeminal nerve intracranially (distally to the semilunar ganglion) were cut too. Later in the experiments the stimulation and recording electrodes could be moved to the main trunk of the hypoglossal nerve.

2. In another series of experiments 36 cats were used, mostly anaesthetized with chloralose 60 mg/kg body weight. In some cases 40–50 mg, in some cases as much as 80 mg/kg was used. Three of the cats were decerebrated under ether. The lingual and hypoglossal nerves were exposed as near their entrance into the tongue as possible and divided. In most experiments the biventer muscle was divided near its insertion and its innervation severed in order to avoid the muscle-twitch of the linguomandibular reflex (CARDOT and LAUGIER 1922).

3. In a third series of experiments 5 cats were used, either decerebrated under ether or anaesthetized with chloralose 60 mg/kg, given intraperitoneally. The glossopharyngeal nerve was identified at the point where it crosses the bulla mastoidea, divided distally to this point, whereupon the nerve was followed proximally as long as possible. The lingual nerves were cut and the hypoglossal nerve was divided. Records were made from the central part of the hypoglossal nerve. The biventer muscle was divided and its innervation destroyed.

4. Seventeen adult cats were used in a fourth series of experiments. Of these cats, seven were decerebrated under ether by an intercollicular section. The extrinsic tongue muscles and the hypoglossal nerve were uncovered. The mouth of the animal was kept open enough by a holder in order to permit the tongue to move freely without touching adjacent structures. The tongue was passively stretched by pulling a thread running through its tip.

The stretch movement was transferred to a potentiometer coupled to a battery. When the slide of the potentiometer moved, a difference in potential was obtained. This difference was fed to a linear amplifier and made visible on one of the oscilloscope beams.

Ten cats were operated upon during ether anaesthesia, curarized and artificially respirated. The hypoglossal nerve was divided as distally as possible. Filaments were isolated from the central end of the divided nerve. From the filaments recordings were made (with the lingual nerves preserved) during mechanical stimulation of various parts of the mouth mucosa.

5. In a fifth series of experiments five cats have been used, anaesthetized with either chloralose (60 mg/kg body weight) or Nembutal (40 mg/kg body weight). After the operation the animals were curarized and artificially respirated. The hypoglossal and lingual nerves were dissected free and divided. The peripheral end of the hypoglossal nerve was stimulated and recordings made from filaments in the peripheral part of the lingual nerve.

These last experiments were performed with the intention to see if any activity set up by stimulation of the hypoglossal nerve was transferred to the lingual nerve via the anastomoses between the two. To avoid the ephaptic potentials which will be set up by the activity in the hypoglossal nerve the animals were curarized (cf. LLOYD 1942).

The stimulation was performed with square waves of about 0.5 msecs duration. When two nerves were stimulated the two shocks were delivered through shielded transformers. The recording device has been described earlier (p. 57). The electromyogram was recorded from the different muscles by steel needles.

The nerves and muscles were continuously flushed with Ringer's solution during the dissection and later during the experiment immersed in paraffin pools at 37° C. The decerebrated animals were kept warm during the experiments, rectal temperature being checked.

## RESULTS

### 1. *Experiments performed with stimulation of and recording from the hypoglossal nerve*

When both the stimulating and recording electrodes were placed on the main hypoglossal trunk before its terminal ramification no signs of a monosynaptic or polysynaptic reflex was ever observed. The stimulation could always be checked by observation of the afferent volley.

However, stimulation of a whole muscle nerve as performed in these experiments has its disadvantages besides the antidromic effect. The different tongue muscles certainly act as antagonists and synergists in different combinations in different movements of the tongue. If, then, all the possibly existing afferents are stimulated at the same time antagonistically acting volleys might be set up. It is possible that in such a case the central effects of this stimulation will cancel each other, so that no efferent activity, i. e. no reflex will be obtained. This problem of different afferents cancelling each other and thereby causing a false result in testing is met with in the case of skin afferents (HAGBARTH 1952) and joint afferents (SKOGLUND 1956).

In order to avoid this source of error, different branches of the hypoglossal nerve were dissected free, stimulated and recorded from in many different combinations. It was not possible in any of these experiments to get a reflex from the hypoglossal nerve.

Other possible explanations for the absence of reflex responses will be discussed in chapter 9.

### 2. *Experiments performed with stimulation of the lingual and recording from the hypoglossal nerve*

When the lingual nerve is stimulated and the recording electrodes placed on the central end of the cut hypoglossal nerve, a reflex is obtained, called the linguo-hypoglossal reflex (BLOM and SKOGLUND 1959).

The latency between the stimulation and the reflex response is about 6 msecs, to some extent depending on the anaesthesia.

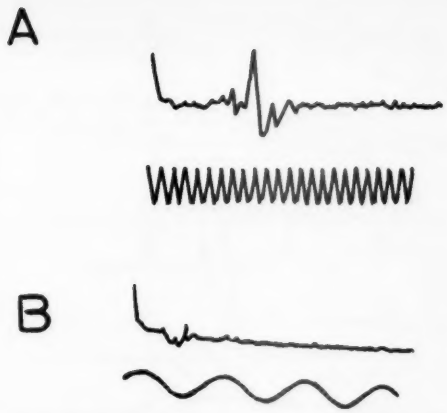



*Fig. 9.* A. Cat, anaesthetized with chloralose, curarized. The linguo-hypoglossal reflex, recorded from the hypoglossal nerve of the same side. Time 1000 cy/sec.
B. Cat, anaesthetized with chloralose, curarized. The linguo-hypoglossal reflex, recorded from small filament of the hypoglossal nerve, same side. Time 100 cy/sec.

The latency is shorter in decerebrated animals, and a little longer (6–7 msecs) in animals anaesthetized with chloralose (Fig. 9 A).

In some experiments the lingual nerve has been dissected free as long as possible by resecting a part of the mandibular bone. In this preparation one recording electrode has been placed on the lingual nerve also in order to measure the conduction velocity with which the afferent impulses giving rise to the linguo-hypoglossal reflex travel (Fig. 10 A). The fibres in the lingual nerve by using HURSH' factor of 6 (HURSH 1939) were calculated to be around 8 microns in diameter (conduction velocity 48 m/sec.). When in some experiments two recording electrodes were placed on the hypoglossal nerve the diameter of the fibres conducting the reflex was in the same way calculated to 6–8 microns (conduction velocity: 36–48 m/sec.) Fig. 10 B. It is perhaps justifiable to make the assumption that the afferent fibres are among the fibres which are held to convey touch in the lingual nerve (ZOTTERMAN 1936) and that the efferent fibres are among the

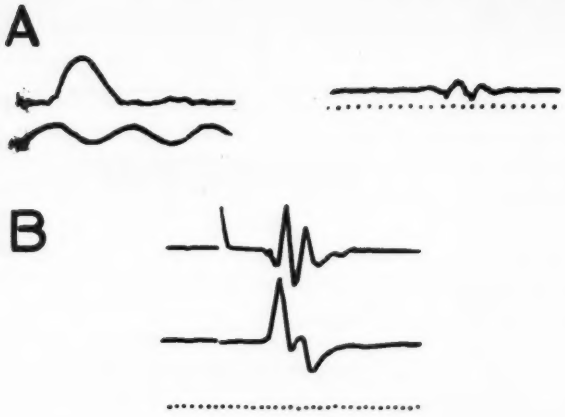



*Fig. 10.* A. Simultaneous recording from the lingual and the hypoglossal nerves to determine size of the reflex-conducting fibres in the lingual nerve. Cat, anaesthetized with Nembutal. *Left*, afferent potential in the lingual nerve. Distance between stimulation and recording electrodes 20 mm. Time 1000 cy/sec. *Right*, reflex in the hypoglossal nerve, recorded at the same time. Time 1000 cy/sec.
B. Two simultaneous recordings of the linguo-hypoglossal reflex. Distance between recording electrodes 25 mm. *Above*, distal recording. *Below*, proximal recording. Time 1000 cy/sec.

motor fibres in the hypoglossal nerve. Such measurements are however always liable to considerable errors.

In one animal the distance between the stimulation point on the lingual nerve and the root entrance of the trigeminal nerve after dissection was measured to be 40–45 mm and the distance between the hypoglossal rootlets and the recording place on the hypoglossal nerve in the same manner measured to 35–40 mm. In this experiment the latency of the reflex was 7 msecs. The central conduction path between the trigeminal root and the hypoglossal roots was measured to about 10 mm. If the diameter of the fibres in the lingual nerve is 8–10 microns, the conduction time in the lingual nerve can in this special case be calculated to 0.7–0.9 msec. The conduction time in the hypoglossal nerve is in the same way calculated to 0.7–1.1 msec. This leaves 5–5.6

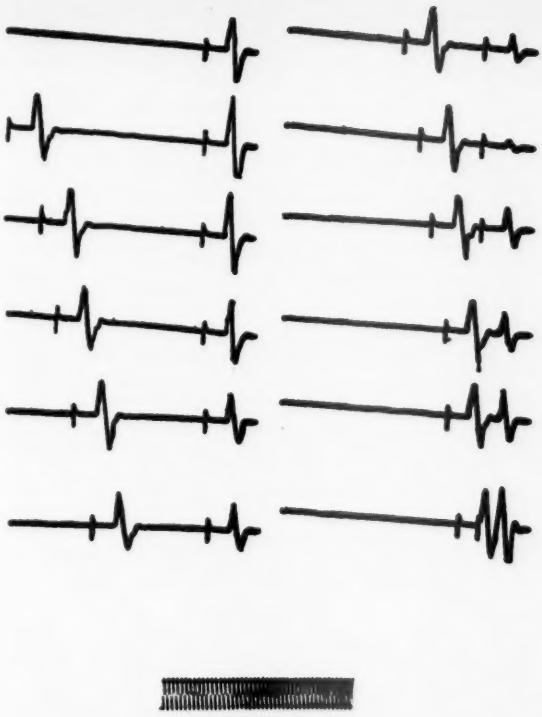


*Fig. 11.* Decerebrated cat. (To be read from above left to below right.) The linguo-hypoglossal reflex, stimulation of ipsilateral lingual nerve. First recording, control. Second and following recordings: reflex elicited twice, conditioning shock moved. Inhibition and facilitation of test shock is shown. Time 1000 cy/sec.

msecs for the central reflex time. The time left for the synaptic delays is then 4.0–4.5 msecs, if the assumption is made that the conduction velocity in the central nervous system amounts to one fifth of the peripheral i. e. in this case around 10 m/sec. (This relationship between peripheral and central conduction velocity has been gained by measurements in the spinal cord, Brooks and Eccles 1947. The central conduction time is in this

case probably longer.) It can thus with a great degree of certainty be said that the linguo-hypoglossal reflex is a polysynaptic reflex. (Cf. p. 67.)

The linguo-hypoglossal reflex is a crossed reflex, i. e. stimulation of the contralateral lingual nerve always evokes the reflex too. In this case the latency however is somewhat increased (in good preparations 0.5–1 msec).

With repetitive stimulation of the lingual nerve on one side, it was found that the possibility to fatigue the reflex is depending on the state of the animal, i. e. the depth of anaesthesia. When testing with two consecutive shocks (Fig. 11) it seems as if a temporal facilitation of approximately 10 msecs' duration occurs. This facilitation is followed by an inhibition, which in good decerebrated preparations lasts about 50 msecs. In more deeply anaesthetized animals (chloralose or Nembutal) the reflex centre can be depressed up to 500 msecs. No detailed measurements have, however, been made on this complex polysynaptic potential, in which the shape of the components is so varying also when supramaximal shocks are applied to the lingual nerve.

The same inhibition-facilitation processes seem to occur also when the shocks are applied one of them on the ipsilateral and the other on the contralateral lingual nerve.

In some animals the hypoglossal nerve was dissected into fine filaments. When the lingual nerve was stimulated it was possible to record a spike in the hypoglossal nerve (Blom and Skoglund 1959), Fig. 9 B.

In a few animals the stimulation was performed by means of electrodes inserted directly into the tongue with intact lingual nerves. Apart from a little longer latency the shape of the reflex was in this case essentially the same.

### 3. *Experiments performed with stimulation of the glossopharyngeal nerve and recording from the hypoglossal nerve*

When the central end of the divided glossopharyngeal nerve is stimulated and a recording is made from the hypoglossal nerve, a reflex with a similar appearance as the linguo-hypoglossal

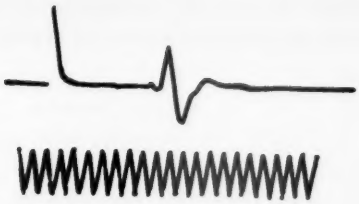


*Fig. 12.* Decerebrated cat. Glossopharyngeo-hypoglossal reflex, recorded from the hypoglossal nerve, same side. Time 1000 cy/sec.

reflex is obtained. This reflex is called the glossopharyngeo-hypoglossal reflex. Fig. 12.

The glossopharyngeo-hypoglossal reflex has a longer latency between stimulation and recording than the linguo-hypoglossal reflex. The difference seems to be around 1 msec. As in the case of the last-mentioned reflex the latency is dependent on the anaesthesia used. It is not possible to place both stimulation and recording electrodes on the glossopharyngeal nerve to measure conduction velocity in order to calculate the size of the fibres stimulated, since the nerve is so deeply situated in the parapharyngeal space. Therefore, no estimation can be made of where in the reflex arch this delay is situated.

The glossopharyngeo-hypoglossal reflex is a crossed reflex too, i. e. it is elicitable from both glossopharyngeal nerves when the recording electrodes are placed on the hypoglossal nerve of one side. The reflex exhibits the same characteristics as the linguo-hypoglossal reflex with regard to inhibition and facilitation when two consecutive shocks are applied to the same side or one of them to the nerve of the other side.

When the glossopharyngeal and the lingual nerves are simultaneously stimulated the reflex response in the hypoglossal nerve is a complex potential with two or three components. When one lingual and one glossopharyngeal nerve are stimulated with two consecutive shocks the same inhibition-facilitation processes occur as when both the conditioning and the test shock are applied to the lingual or glossopharyngeal nerve alone.

4. *Experiments performed with stimulation of the tongue and recording from the tongue muscles or the hypoglossal nerve*

In the decerebrated animals where electromyographic recordings were made from the tongue muscles during different stimulations of the tongue, the following observations were made.

In a good decerebrated animal with normal extensor hypertonus and with normal breathing, no signs of activity can be recorded at rest in the different tongue muscles by electromyography. If the animal is hyperventilating, which is usually a sign of bleeding from the brainstem section backwards and downwards around the brainstem, almost always spontaneous activity related to the breathing appears in the tongue muscles. Such animals have not been used in the investigation.

When the lower jaw is opened, in a good preparation, activity appears in the tongue muscles (Fig. 13 A). This activity is evidently related to the stretch of the masseter muscles, since it disappears when these muscles are divided. It does not appear, until the jaw is opened a few centimetres and then increases with increasing jaw movement. When the jaw is released, the activity instantly disappears.

In some animals it was necessary to cut the masseter muscles to be able to open the jaw sufficiently to handle the tongue without having this initial masseter-induced activity in the tongue muscles. Section of the jaw-opening digastric muscle did not influence the results.

When the jaw was kept slightly open and the tongue stretched by a pull at a thread through the tip (Fig. 13 C) no activity could be recorded from the tongue muscles. When on the other hand the movement was established by a forceps clasping the tongue, activity could be registered. It could be registered in each of the extrinsic muscles and in different parts of the intrinsic muscles each of which cannot for obvious reasons be studied separately by this method.

When the lingual and glossopharyngeal nerves were cut no activity in the tongue muscles could be recorded either by stretch or by any other way of handling the tongue.

Ten animals were curarized after the operation and dissection,

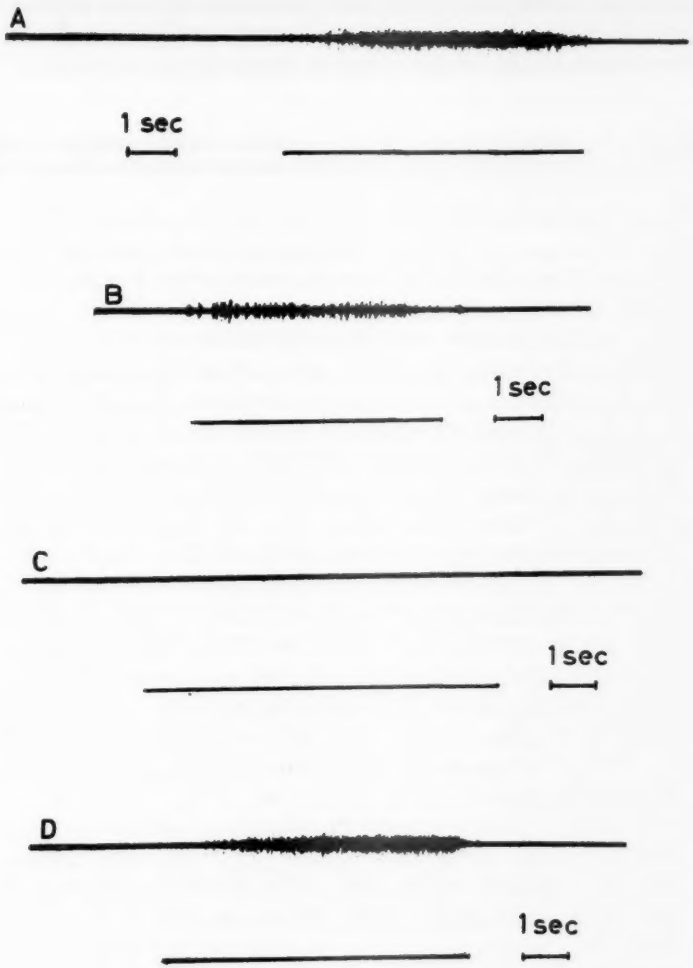



*Fig. 13.* Decerebrated cat. Electromyographic recordings from the intrinsic tongue muscles during A) downward movement of the lower jaw, B) clasping of the tongue by a forceps, C) stretch of the tongue by a pull at a thread through its tip and D) downward movement of the lower jaw, control. Stimulation indicated by signal line.

which was performed during ether anaesthesia. In these animals, recordings were made from isolated hypoglossal filaments during stimulation of the tongue surface mechanically.

*Fig. 14.* Curarized cat. Recording from filament of the hypoglossal nerve during and after stimulation of the tongue surface, indicated by signal line. Time 50 cy/sec.

Under these circumstances in most of the hypoglossal filaments a certain amount of resting activity can be recorded. When the tongue is touched, bursts of activity appear in the hypoglossal filaments synchronously with the touch upon the tongue. Between the bursts no resting activity can be recorded. This burst-shaped activity continues after the moment when the stimulation of the lingual mucosa has ceased. This event is shown in Fig. 14, recorded from a hypoglossal filament without resting activity. The burst-shaped activity is clearly seen, occurring both during and after the stimulation. The tongue was in this case only slightly touched by a piece of cotton-wool. The same sort of activity can be registered during and after touch applied to the hard palate. In the curarized animals no activity could be recorded in hypoglossal nerve filaments in response to movements of the jaw.

In some animals, especially in those with small or no resting activity, spikes which are synchronous with the artificial breathing of the animal can be recorded. This activity has not been further investigated during this work.

5. *Experiments performed with stimulation of the hypoglossal nerve and recording from the lingual nerve*

After curarization recording was made from filaments of the lingual nerve with stimulation of the peripheral end of the cut hypoglossal nerve. Many different lingual nerve filaments were

used in the experiments but in none of these action potentials could be recorded, which could derive from fibres belonging to the anastomoses between the lingual and the hypoglossal nerves.

## DISCUSSION

The experiments have shown the reflexes between the lingual, glossopharyngeal and hypoglossal nerves.

As regards the afferents in the hypoglossal nerve, described on p. 57, efforts have been made to study them by other physiological methods. If the afferents were confined to the hypoglossal nerve, it ought to be possible to record reflex activity in the hypoglossal nerve, when this nerve is stimulated. This has not been the case. As they follow the hypoglossal nerve at least for a short distance, even if they are transferred to the lingual nerve, experiments were also performed with stimulation of the peripheral end of the hypoglossal and recording from the distal end of the lingual nerve in curarized animals. However, these experiments did not succeed, i. e. no activity could be recorded in the lingual nerve. This can perhaps be due to anatomical variations from one animal to another, as it seems as if the anastomoses occurring proximally, i. e. outside the tongue are rather infrequent. As a final statement regarding these fibres it must however be admitted that no definite proof can be given as concerns their origin and course.

The lingual nerve has earlier been regarded as a possible afferent channel for impulses acting upon the hypoglossal nerve (Schoen and Koeppen 1931, Barron 1936, Tarkhan 1936, Corbin and Harrison 1938). That the glossopharyngeal nerve takes part in this innervation can be suspected from the fact that it innervates the posterior third of the tongue in the same manner as the lingual nerve innervates the anterior two thirds. The glossopharyngeal nerve is however probably not as important as the lingual nerve with regard to its reflex connections with the hypoglossal nerve. The calibre measurements of the glossopharyngeal nerve have shown that the percentage of large fibres is not so great in this nerve as in the lingual. It has

not been possible to show that these fibres actually give rise to the glossopharyngeo-hypoglossal reflex, but it may be regarded as logical to compare the two reflex-arcs from this point of view and make this assumption.

The reflexes described are polysynaptic reflexes, which can be calculated from the measurements of the reflex time. Their general appearance moreover resembles that of the polysynaptic reflexes, which are found in the spinal cord. This and the absence of a monosynaptic reflex path again points to the absence of muscle spindles in the tongue muscles.

By measurement of the conduction velocity of the fibres in the lingual nerve it has been shown that with all probability the largest fibres of the nerve contribute to the afferent part of the reflex arc. These are (as has been shown by ZOTTERMAN 1936) touch and pressure fibres, but have also here (cf. p. 59) been shown to fire in response to a contraction of the tongue muscles. It is of course very possible that smaller fibres conveying pain are activated when the lingual nerve is stimulated, thus contributing to the reflex.

In conformity with the earlier described experiments (cf. p. 58) it has not been possible to record any activity from the tongue muscles by electromyography during stretch of the tongue. Again, as soon as touch comes in, activity can be detected in the tongue muscles. That the impulses which influence the hypoglossal nerve are transferred via the lingual and glossopharyngeal nerves can be concluded from the fact that the activity ceases as soon as these nerves are divided. The advantage of the electromyographic experiments described here is that no interference with the nerve supply is necessary and further that the stimulation is as adequate as possible.

The animals in which recordings have been made by electromyography, have been decerebrated, an operation which might alter also the excitability of the hypoglossal motoneurones. This was the reason for the use of curarized animals, in which however essentially the same results were obtained. In these experiments the recording for natural reasons was however made from the hypoglossal nerve. The spontaneous activity seen in these animals might give rise to a tonic activity in the tongue muscles. The

bursting activity observed after cessation of the stimulus can be induced from other afferent sources playing upon the hypoglossal motoneurones. The reason why the burst-shaped activity appears in response to touch in the curarized animals but not in the decerebrated animals is difficult to settle with certainty. It is possible that in the curarized animals touch induces also other movements in which the tongue takes part, as for instance swallowing, which for obvious reasons cannot be observed in this preparation. In decerebrated animals such movements have never been observed and no bursting activity has been recorded. One difference between these experiments and the observations made in decerebrated preparations is the absence of activity induced by movements of the lower jaw. The explanation for this might be that in a curarized animal both the alpha and gamma motor end plates are blocked (GRANIT, SKOGLUND and THESLEFF 1952). This means a lowered spindle bias, from which follows that the afferent activity from the masseter muscles is considerably lowered (GRANIT and HENATSCH 1956). The curarized animals behave in this respect as decerebrated animals with divided masseter muscles.

It must be emphasized that the effects produced in the hypoglossal nerves or the tongue muscles have not been analysed with regard to movements of the tongue, which are produced by the various afferent impulses. Reflexes such as the linguo-hypoglossal and glossopharyngeo-hypoglossal are mass reflexes, and can tell nothing about the actual movements of the tongue. The important thing is however that such reflex pathways exist.

## SUMMARY

In this chapter the effects of stimulation of the tongue or the tongue nerves upon the hypoglossal nerve and the tongue muscles have been studied. The results can be summarized as follows:

1) It has not been possible to record any reflex activity in the hypoglossal nerve after stimulation of the whole hypoglossal nerve or its branches. It has however not been possible to settle with certainty the course of the afferents

found in the peripheral course of the hypoglossal nerve, earlier described.

2) Reflexes called the linguo-hypoglossal and the glosso-pharyngeo-hypoglossal reflexes respectively have been demonstrated and their properties are discussed.
3) Impulse activity can be recorded in single fibre preparations of the hypoglossal nerve or in the tongue muscles during various types of mechanical stimulation of the tongue.

CHAPTER 9

# Antidromic Effects from one Hypoglossal Branch upon another

TARKHAN (1936 b) in experiments, which are similar to those going to be described here, obtained reflex movements of the tongue when he stimulated the central end of the cut medial end branch of the hypoglossal nerve, with the rest of the innervation to the tongue preserved.

RENSHAW (1941) demonstrated the effect on spinal reflexes of antidromic shocks applied to partly divided ventral roots of the spinal cord. He found the effect to be varying, sometimes facilitatory, sometimes inhibitory. In some cases no effect at all could be demonstrated. RENSHAW later (1946) suggested that these effects were mediated via recurrent collaterals from motor axons and interneurones, firing at very high frequencies. This has later (1953) been confirmed by ECCLES, FATT and KOKETSU. GRANIT, PASCOE and STEG (1957) found the recurrent inhibition to be one possible mechanism, by which the output frequency of the tonic ventral horn cells can be maintained at a low level. WILSON, TALBOT and DIECKE (1959) showed in conformity with RENSHAW's original finding that the recurrent collaterals have both facilitatory and inhibitory effects, which seem to act in a reciprocal manner with regard to the muscles.

CAJAL (1909) described recurrent collaterals from motor axons in the spinal cord, but could not find such collaterals from the hypoglossal axons in man.

As the hypoglossal nerve has no dorsal root, the nerve can be regarded as equivalent to a ventral root in the spinal cord. Experiments have been performed to investigate if recurrent inhibition similar to that in the spinal cord ventral roots can be demonstrated in the hypoglossal motoneurones, which would signify that these motoneurones are furnished with recurrent collaterals.

## MATERIAL AND METHODS

Decerebrated cats were used. For technical reasons the roots of the hypoglossal nerve cannot be used for stimulation. Therefore, part of the hypoglossal nerve (usually the main branch to the intrinsic muscles) was dissected free and divided. The rest of the innervation to the tongue muscles was preserved. Activity in these muscles was set up by a slight opening of the lower jaw, not changed during the experiment. This activity was recorded by steel electrodes inserted into the muscle. The central end of the cut branch was then stimulated and the effect of the stimulation was studied on the electromyographic activity of the tongue muscles with preserved innervation.

The stimulation and recording device has earlier been described.

## RESULTS

In all the experiments performed, an inhibition of the activity in the muscles with preserved innervation could be obtained, when conditioning with a recurrent stimulation which was applied to another part of the hypoglossal nerve. This inhibition

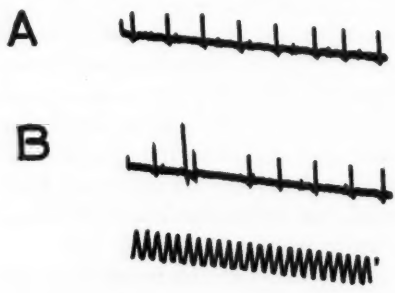



*Fig. 15.* Decerebrated cat, electromyographic recording from the styloglossal muscle, showing A) activity induced by slight downward movement of the lower jaw and B) inhibition of this activity by recurrent stimulation of the hypoglossal branch to the intrinsic muscles. Time 50 cy/sec.

*Fig. 16.* Decerebrated cat. Electromyographic recording of mass activity in the hyoglossal muscle, showing A) activity induced by slight downward movement of the lower jaw and B) inhibition of this activity by recurrent stimulation of the hypoglossal branch to the intrinsic muscles. Time 100 cy/sec.

was studied both on single motoneurones and on mass activity (Fig. 15, 16). Some motoneurones, however, were found which were uninfluenced and thus not recurrently inhibited. The period of total inhibition is usually around 20 msecs.

## DISCUSSION

Principally the same method as that applied in the experiments described here was used by HOLMGREN and MERTON (1953) for demonstrating recurrent inhibition. These authors found a total inhibition of a background activity (set up by pinching the opposite flank) in the de-afferented soleus muscle of decerebrated cats by antidromic shocks applied to the medial gastrocnemius nerve.

Spread of current leading to antidromic activation of the whole hypoglossal nerve has been carefully avoided. The latency between stimulation and inhibition is too long for an antidromic effect. Furthermore, as shown by LLOYD (1943), antidromic activation does only lead to complete inhibition when the volleys clash in the motor axons. This is very unlikely to occur in an

experiment like the one described here, where a continuous impulse traffic is going on. In this case a complete inhibition is obtained.

The inhibition found might be set up by afferents in the hypoglossal nerve. On account of the negative findings in the experiments performed with stimulation of different branches of the hypoglossal nerve and recording from others in many combinations (see p. 66) it must be assumed that these afferents should then have only inhibitory effects. This seems highly improbable. Moreover, most of other morphological and physiological results earlier described contradict the existence of any afferent system in the hypoglossal nerve: the results from the calibre measurements and fibre counts, the failure of finding afferent activity during stretch of the tongue in the main hypoglossal trunk etc.

It can also here be stated that the recurrent inhibition has too long a latency to be the explanation of the negative outcome of the reflex experiments described on p. 66. If a reflex pathway existed in the hypoglossal nerve, a reflex ought to be elicitable during the 15 msecs which precede the antidromic inhibition.

Although definite morphological evidence for the existence of recurrent collaterals from the axons of the hypoglossal nerve of the cat is lacking and physiological experiments using the prolongating effect on recurrent inhibition of eserine sulphate cannot be used on account of its simultaneous effect on the muscle, it appears more likely that this inhibition is set up by recurrent collaterals than by an afferent system with exclusively inhibitory effects. Trials to test the inhibition on the linguo-hypoglossal reflex, in which eserine sulphate could be used, must be omitted owing to the great variability of this reflex.

The inhibition and rebound seen in Fig. 16 can however explain the reflex movements of the tongue observated by TARKHAN (1936 b).

CHAPTER 10

# The Relationship between the Jaw-moving and the Tongue Muscles

The relations between the jaw-moving muscles and the tongue muscles have previously been studied by SCHOEN (1931), SCHOEN and KOEPPEN (1931). Their investigations were performed on thalamic or decerebrated cats and the reflex movements were registered. SCHOEN (1931) reported that reflex movements of the tongue were recordable when the jaw was opened against the resistance of the jaw-closing muscles. These movements were thought to be evoked by activation of stretch receptors in the masseter muscles, because they did not appear when a bilateral anaesthesia of the mandibular nerve at foramen spinosum was made. Active opening of the jaw (performed by contraction of the digastric muscle) was not accompanied by any movement of the tongue and division of the digastric muscle did not influence the tongue movements produced by jaw-opening against resistance. SCHOEN further noticed the linguo-mandibular reflex (first described by CARDOT and LAUGIER 1922), in which a stimulation of the tongue surface evokes a reflex in the digastric muscle, and pointed out that tongue movements could be observed in connection with this reflex.

Muscle spindles have been described in the chewing-muscles of man by FREIMANN (1954). With regard to their existence in the digastric muscle different findings have been reported. BAUM (1900) and GREGOR (1904) denied their existence, but VOSS (1956) described a few spindles in the anterior part but did not find any in the posterior part of the muscle in man. Concerning the cat, information can be obtained from the work by SZENTÁGOTHAI (1948). After destruction of the mesencephalic tract of the trigeminal nerve, he found degeneration in the nerves to the masseter, temporalis and pterygoideus muscles (and degenerated muscles spindles in the masseter muscle) but no de-

generated nerve fibres in the nerves to the mylohyoid, digastric and tensor muscles. SZENTÁGOTHAI did evidently not search for muscle spindles in the digastric muscle, but since degeneration was absent in the nerve to this muscle in his experiments, it must be suspected that they are missing in this muscle.

## MATERIAL AND METHODS

The experiments were performed on thirteen cats. Seven of these were decerebrated. In these decerebrated animals the electromyogram of the masseter muscle was recorded during opening of the lower jaw. The electromyogram was further recorded in different tongue muscles also during opening of the jaw. The lingual nerve was then divided bilaterally and the influence of jaw-opening upon the tongue muscles was recorded once more, both with and without denervated digastric muscle. In some experiments that part of the mandible was removed upon which the insertion of the digastric muscle is situated, whereupon the muscle was stretched with electrodes in the muscle to examine if any stretch reflex was obtained.

Six of the animals were anaesthetized with chloralose 60 mg/kg body weight and the nerves to the masseter and biventer muscles, the lingual and the hypoglossal nerves were dissected free and divided. The central ends of the cut nerves were stimulated and recordings made on the others one by one to see if any reflex effects could be obtained.

The electromyogram was recorded by means of two steel electrodes insulated to the tip. The stimulation and recording device was the same as earlier described.

## RESULTS

The results, which were similar in nature in every experiment performed, were as follows.

When the jaw is opened in an intercollicularly decerebrated cat activity can be recorded from the masseter muscle. How much the jaw has to be opened, i. e. how much the masseter muscle has to be stretched, has often but not always been found

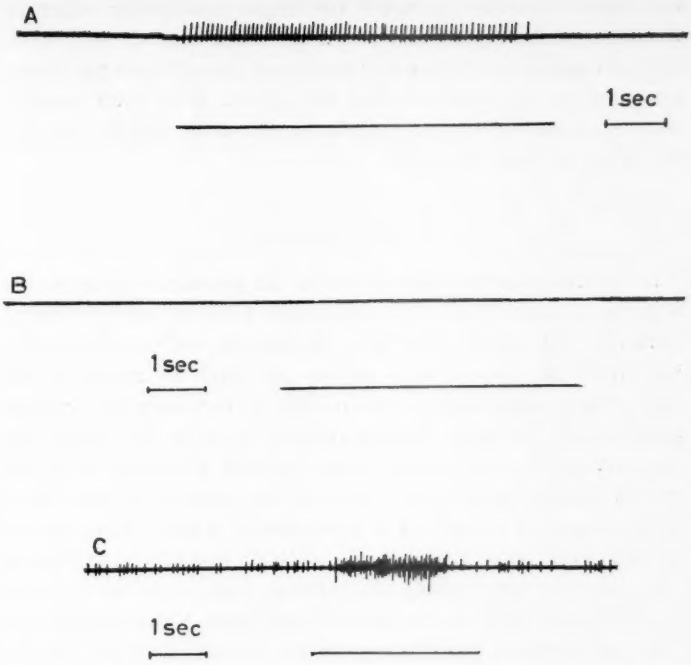



*Fig. 17.* Decerebrated cat. A) Recording from the styloglossal muscle showing one active motor unit in response to downward movement of the lower jaw. B) Recording from the same muscle during stretch of the digastric muscle. C) Recording from the hyoglossal muscle during downward jaw-movement. In this case a certain resting activity is seen before and after the movement. Movements of the jaw indicated by signal line.

to depend upon the degree of excitability in the masseter motoneurones.

When the jaw is opened in an intercollicularly decerebrated cat and the recording electrodes are placed in different tongue muscles, activity can be recorded from these. (See Fig. 17.)

No stretch-reflex has been found in the digastric muscle. Stretch of the muscle does not induce any activity in the tongue muscles.

In the animals which were anaesthetized with chloralose, it

was always possible to record the linguo-mandibular reflex in the nerve to the digastric muscle after stimulation of the lingual nerve. Stimulating the digastric nerve and recording on the hypoglossal nerve has never revealed any reflex. When both stimulation and recording are made on the nerves to the digastric muscle, no reflex has been recorded.

## DISCUSSION

A stretch reflex has been found in the masseter but not in the digastric muscle. This is in conformity with the morphological results by SZENTÁGOTHAI (1948). He showed that muscle spindles are present in the masseter muscle but from his results in the degeneration experiments one is apt to conclude that muscle spindles are missing in the jaw-opening muscles. As regards the digastric muscle there seems to be a species difference, as a few muscle spindles have been found in this muscle in man (Voss 1956). The only recordings in that muscle in man known to the author, were performed by CARLSÖÖ (1956). His investigation was however performed on persons who were awake and obviously not with the purpose of recording a stretch reflex in the muscle, but of studying voluntary activation of this muscle and the other mandible-moving muscles.

The decerebrated animal might not be the ideal preparation for recording a stretch reflex in the digastric muscle, because this muscle can be regarded as a flexor (KING, MINZ and UNNA 1955). Contrary to this the masseter muscle behaves as an extensor muscle. No reflex activity was obtained when stimulating and recording from the nerve to the digastric muscle. This and the findings reported by SZENTÁGOTHAI (1948) suggest that the digastric muscle is not capable of influencing the hypoglossal motoneurones in an excitatory way.

From the experiments can further be gathered that the masseter muscle influences the tongue muscles and that this influence is probably set up by the input from its spindles. Thus there exists a relationship between tonus in the jaw-closing muscles and the activity of the tongue muscles. This is a confirmation of the results published by SCHOEN (1931).

## SUMMARY

It seems as if the influence of the jaw-moving muscles upon the tongue muscles is restricted only to the jaw-closing muscles. The jaw-opener, the digastric muscle, on the other hand is influenced both from the masseter muscle and from the tongue.

# General Comments and Conclusions

The results obtained during this investigation have been separately discussed in the sections dealing with the different experiments. The experimental results which seem to be particularly relevant will here be synthetized.

The major part of earlier evidence strongly supports the view that muscle spindles are absent in the tongue muscles of various animals, even if their presence has been described by some authors (LANGWORTHY 1924 b, TARKHAN 1936 a). Their findings have been the basis for much work later done in this field. It seemed therefore important to start this investigation with a study of the tongue muscles of the cat in this respect.

No muscle spindles were found, neither in the intrinsic nor in the extrinsic muscles. This result, a confirmation of many earlier works (cf. p. 17), is compared with the results of investigations of the tongue nerves with regard to their fibre size and connections. These studies did not, either in the hypoglossal, the lingual or the glossopharyngeal nerves, reveal fibres that, according to our present-day knowledge, can with certainty be held to be nuclear bag afferents from muscle spindles situated in the intrinsic muscles. There are a few big fibres in the hypoglossal nerve, but their destination has been found to be the extrinsic muscles. Physiological experiments however showed that these fibres are with all probability efferent and not afferent.

In this connection it is important to discuss the possible existence of other sense organs than muscle spindles in the extrinsic tongue muscles (WEDDELL et al. 1940), the nerve cells found scattered along the hypoglossal nerve (TARKHAN 1936 a), as well as the end organs described by LAW (1954). It is very difficult to draw any conclusion about the function of an end

organ or about the function of a nerve cell only from their morphology. The author will not deny the possible afferent properties of these structures, but it is very unlikely that they play an important role in the regulation of tongue movements. This opinion is supported by the negative results of the physiological studies. The only physiological evidence of their existence is the afferent activity found in the peripheral part of the hypoglossal nerve, first described by COOPER (1954), and confirmed during this work. The fibres from these end organs can reach the central nervous system either by way of the hypoglossal nerve or the lingual nerve via the peripheral connections between the two. Experiments have been performed to study and evaluate the importance of these afferent pathways further by physiological methods, but no definite evidence can be presented that permits a final statement about their way to the central nervous system and the role played by them in the regulation of the tongue movements. However, it seems important to point out that no reflex activity has been observed when both stimulation and recording are made on the hypoglossal nerve.

All morphological and physiological evidence in this investigation contradicts the existence of a muscle spindle system in the tongue of the cat. The morphological findings also indicate that in earlier investigations described connections between the hypoglossal nerve and other cranial nerves or the cervical nerves must have other functional tasks than contributing to the reflex control of the tongue muscles. This statement can be made as it has been shown here that the hypoglossal nerve does not change either its number of fibres significantly or its composition with regard to fibre size between the hypoglossal canal in the occipital bone and its terminal ramifications. No dorsal root belonging to the hypoglossal nerve has been observed during this investigation, and those described by LANGWORTHY (1924 b) and HOLLIGER (1955) cannot possibly contain muscle spindle afferents, since most of their fibres are very small according to LANGWORTHY.

Thus, much evidence suggests that the lingual and glossopharyngeal nerves are the main, perhaps even the only afferent channels from the tongue, through which influence can be exerted

upon the hypoglossal motoneurones. In conformity with this, reflexes here found in the hypoglossal nerve in response to stimulation of the nerves in question, and activity set up in the tongue muscles by mechanical stimulation of the tongue, were abolished by dividing these nerves.

As no ordinary stretch receptor system could be detected in the tongue, a substitute that could be revealed by physiological methods, was searched for. It has been confusing that passive stretch of the tongue muscles, as accomplished by pulling the tongue, never has given rise to afferent activity in the lingual or glossopharyngeal nerves. It has here been shown that the proper way of revealing activity, set up by muscle activity, in these nerves is to establish a short, phasic contraction of the tongue muscles by stimulation of the hypoglossal nerve. When this is done end organs, with all probability situated in the submucosal tissue of the tongue, are activated. These end organs behave as stretch receptors, and, being rapidly adapting, respond to phasic movements of the tongue muscles. They can of course also be activated by direct pressure and touch.

It seems reasonable to separate tonic activity from phasic activity also in the hypoglossal motoneurones. The tonus of the tongue is very important for instance in holding the air-passage free. The tonic activity of the hypoglossal motoneurones is probably set up from different sources, among which the respiratory influences probably play an important role. This mechanism has not been further studied during this investigation.

Phasic activity of the tongue muscles in an anaesthetized animal without voluntarily induced movements can be initiated reflexly from the periphery. Of this phasic activity mainly that which can be produced from the tongue itself has been studied here. It has also been shown that the tongue can be influenced by stimulation of end organs in the mouth mucosa. It was found that the same rapidly adapting sense organs that respond to touch and similar mechanical stimulation (ZOTTERMAN 1936) can also be activated by fast movements of the tongue. However, also other muscular activity, that of the jaw-muscles, acts upon the tongue muscles. It was found, in agreement with the experiments by SCHOEN (1931), that of the jaw-moving muscles only

the jaw-closers act upon the tongue. This probably means that phasic movements of these muscles (as for example in chewing) are reflected in the tongue. It is interesting to note that these muscles are equipped with muscle spindles.

The phasic activity which as shown here can be produced in the tongue muscles by different types of afferent stimulation is probably of great importance with regard to tongue movements. It is the way by which the position of the tongue can rapidly be changed as a result of afferent influences from various sources, including the tongue itself.

If the human tongue and its movements is arranged in the same way, is difficult to state as physiological evidence is lacking. The movements of the human tongue are complicated by its participation in speech and furthermore by the more complicated structure of the jaw movements. The physiological significance of the muscle spindles described by COOPER (1953) in the human tongue cannot be evaluated either. The calibre measurements performed by REXED (1944) of the hypoglossal nerve in man show a calibre spectrum that is very similar to that of the same nerve in the cat, even if the peak of the spectrum is somewhat higher situated in the former case. The hypoglossal nerve of man has no more than that of the cat a dorsal root. These circumstances perhaps justify the final statement that the hypoglossal nerve neither in man nor in the cat is a sensori-motor nerve in the same meaning as the muscle nerves to other striated musculature.

# References


Abd-el-Malek, S., Observations on the morphology of the human tongue.
J. Anat., Lond. 1939. *73.* 201–210.

Barker, D., The innervation of the muscle spindles.
Quart. J. micr. Sci. 1948. *89.* 143–186.

Barnard, J. W., The hypoglossal complex of vertebrates.
J. Comp. Neurol. 1940. *72.* 489–524.

Barron, D. H., A note on the course of the proprioceptor fibres from the tongue.
Anat. Rec. 1936. *66.* 11–15.

Batten, F. E., The muscle spindle under pathological conditions.
Brain 1897. *20.* 138–179.

Baum, J., Beiträge zur Kenntnis der Muskelspindeln.
Anat. Hefte 1900. *13.* 251—305.

Blom, S. and S. Skoglund, Some observations on the control of the tongue muscles.
Experientia 1959. *15.* 12.

Boeke, J., Die morphologische Grundlage der sympatischen Innervation der quergestreiften Muskelfasern.
Zschr. mikr. anat. Forsch. 1927. *8.* 561—640.

Boyd, J., Proprioceptive innervation of mammalian tongue.
J. Anat., Lond. 1937. *72.* 147–148.

— The sensory component of the hypoglossal nerve in the rabbit.
J. Anat., Lond. 1941. *75.* 330–346.

Brooks, C. McC. and J. C. Eccles, Electrical investigation of the monosynaptic pathway through the spinal cord.
J. Neurophysiol. 1947. *10.* 251–273.

Cajal, R. y, Histologie du Système nerveux I. A. Maloine, Paris 1909.

Cardot, H. and H. Laugier, Le réflexe linguo-maxillaire.
C. rend. Soc. biol. 1922. *86.* 529—530.

Carleton, A., Observations on the problem of the proprioceptive innervation of the tongue.
J. Anat., Lond. 1937. *72.* 502–507.

Carlsöö, S., An electromyographic study of the activity of certain suprahyoid muscles (mainly the anterior belly of the digastric muscle) and of the reciprocal innervation of the elevator and depressor musculature of the mandible.
Acta Anat., Basel. 1956. *26.* 81–93.

Casasco, E., Circa la presunta componente sensitiva del nervo ipoglosso. Boll. Soc. ital. biol. sper. 1951. *27*. 1497–98.

Clara, M., Das Nervensystem des Menschen. J. A. Barth, Leipzig 1953. p. 342.

Cohen, M. J., S. Landgren, L. Ström and Y. Zotterman, Cortical reception of touch and taste in the cat. A study of single cortical cells. Acta physiol. scand. 1957. *40*. suppl. 135.

Cooper, S., Muscle spindles in the intrinsic muscles of the human tongue. J. Physiol., Lond. 1953. *122*. 193–202.

— Afferent impulses in the hypoglossal nerve on stretching the cat's tongue. J. Physiol., Lond. 1954. *126*. P 32.

Cooper, S., P. Daniel and D. Whitteridge, Muscle spindles and other sensory endings in the extrinsic eye muscles: the physiology and anatomy of these receptors and of their connexions with the brain-stem. Brain 1955. *78*. 564–583.

Corbin, K. B. and F. Harrison, Further studies on tongue innervation. Proc. Soc. Exp. Biol., N. Y. 1938. *38*. 308–310.

— The sensory innervation of the spinal accessory and tongue musculature in the rhesus monkey. Brain 1939. *62*. 191–197.

Corbin, K. B., W. T. Lhamon and D. W. Petit, Peripheral and central connections of the upper cervical dorsal root ganglia in the rhesus monkey. J. Comp. Neurol. 1937. *66*. 405–414.

Daniel, P., Sensory nerve endings in the extrinsic eye muscles of man. J. Anat., Lond. 1946. *80*. 189–193.

Downman, C. B. B., Afferent fibres of the hypoglossal nerve. J. Anat., Lond. 1939. *73*. 387–395.

Eccles, J. C., P. Fatt and K. Koketsu, Cholinergic and inhibitory synapses in a central nervous pathway. Austr. J. Sci. 1953. *16*. 50–54.

Eccles, J. C. and C. S. Sherrington, Numbers and contraction-values of individual motor units examined in some muscles of the limb. Proc. R. Soc. 1930. *106 B*. 326–357.

Fernand, V. S. V. and J. Z. Young, The sizes of the nerve fibres of muscle nerves. Proc. R. Soc. 1951. *139 B*. 38–58.

FitzGerald, M. J. T. and M. E. Law, The peripheral connexions between the lingual and hypoglossal nerves. J. Anat., Lond. 1958. *92*. 178–188.

Forster, L., Zur Kentniss der Muskelspindeln. Virchows Arch. 1894. *137*. 121—154.

Freimann, R., Untersuchungen über Zahl und Anordung der Muskelspindeln in den Kaumuskeln des Menschen. Anat. Anz. 1954. *100*. 258—263.

FRORIEP, A. and W. BECK, Ueber das Vorkommen dorsaler Hypoglossuswurzeln mit Ganglion, in der Reihe der Säugetiere.
Anat. Anz. 1895. *10*. 668—696.

GAIRNS, F. W., Sensory nerve endings other than taste buds in the human tongue.
J. Physiol., Lond. 1953. *121*. 33–34 P.

GRANIT, R., Receptors and sensory perception. New Haven. Yale University Press. 1955.

GRANIT, R., and H. D. HENATSCH, Gamma control of dynamic properties of muscle spindles. J. Neurophysiol. 1956. *19*. 356–366.

GRANIT, R., J. E PASCOE and G. STEG, The behaviour of tonic alpha and gamma motoneurones during stimulation of recurrent collaterals.
J. Physiol., Lond. 1957. *138*. 381–400.

GRANIT, R., O. POMPEIANO and B. WALTMAN, The early discharge of mammalian muscle spindles at onset of contraction.
J. Physiol., Lond., 1959, *147*, 399–418.

GRANIT, R. and B. REXED, Om afferenta effekter i ryggmärgens bakre rötter, Ett undantag från Bell-Magendies lag?
Nord. med. 1942. *16*. 2899–2908.

GRANIT, R., S. SKOGLUND and S. THESLEFF, Activation of muscle spindles by succinylcholine and decamethonium. The effects of curare.
Acta. physiol. scand. 1953. *28*. 134–151.

GREGOR, A., Ueber die Vertheilung der Muskelspindeln in der Muskulatur des menschlischen Fötus.
Arch. Anat. 1904. 112—196.

HAGBARTH, K.-E., Excitatory and inhibitory skin areas for flexor and extensor motoneurones.
Acta physiol. Scand. 1952. *26*. suppl. 94.

HAGBARTH, K.-E. and G. WOHLFART, The number of muscle-spindles in certain muscles in cat in relation to the composition of the muscle nerves.
Acta Anat., Basel. 1952. *15*. 85–104.

HAMMOND, W. S. and J. C. HINSEY, The diameters of the nerve fibres in normal and regenerating nerves.
J. Comp. Neurol. 1945. *83*. 79–89.

HENSEL, H., and Y. ZOTTERMAN, The response of mechanoreceptors to thermal stimulation.
J. Physiol., Lond., 1951, *115*, 16–24.

HEWER, E. E., The development of nerve endings in the human foetus.
J. Anat., Lond. 1935. *69*. 369–379.

HINSEY, J. C. and K. B. CORBIN, Observations on the peripheral course of the sensory fibres in the first four cervical nerves in the cat.
J. Comp. Neurol. 1934. *60*. 37–44.

HOLLIGER, A., Contribution à l'étude de la constitution de l'anse du nerfe hypoglosse; étude d'anatomie comparée.
Arch. Anat. Hist. Embr. 1955. *38*. 4–46.

Holmgren, B., and P. A. Merton, Local feedback control of motoneurones. J. Physiol., Lond., 1953, *123*, 47–48P.

Hursh, J. B., Conduction velocity and diameter of nerve fibres. Amer. J. Physiol., 1939, *127*, 131–139.

Häggqvist, G., A contribution to the question of the nerves and muscular substratum of the muscle tone. Acta med. scand. 1940. *104*. 8–20.

Jansen, J. and A. Brodal, Aspects of cerebellar anatomy. Oslo, J. G. Tanum 1954. p. 158.

Kimmel, D. L., Differentiation of the bulbar motor nuclei and the coincident development of associated root fibres in the rabbit. J. Comp. Neurol. 1940. *72*. 83–148.

King, E. E., B. Minz and K. R. Unna, The effect of the brain stem reticular formation on the linguomandibular reflex. J. Comp. Neurol. 1955. *102*. 565–596.

Kiss, F. and P. v. Mihàlik, Die Zusammensetzung der peripherischen Nerven und der Zusammenhang zwischen Morphologie und Funktion der peripheren Nervenfasern. Zschr. ges. Anat. 1928. *88*. 112–151.

Kopsch, F., Rauber-Kopsch, Lehrbuch und Atlas der Anatomie des Menschen II. G. Thieme, Leipzig 1955. p. 484.

Landgren, S., Convergence of tactile, thermal and gustatory impulses on single cortical cells. Acta physiol. scand. 1957. *40*. 210–221.

Langworthy, O. R., Problems of tongue innervation: course of proprioception and autonomic innervation of skeletal musculature. Bull. Johns Hopkins Hosp., 1924 a. *35*. 239–246.

— A study of the innervation of the tongue musculature with particular reference to the proprioceptive mechanism. J. Comp. Neurol. 1924 b. *36*. 273–297.

Law, M. E., Lingual proprioception in pig, dog and cat. Nature 1954. *174*. 1107–08.

Lloyd, D., Stimulation of peripheral nerve terminations by active muscle. J. Neurophysiol. 1942. *5*. 153–165.

— The interaction of antidromic and orthodromic volleys in a segmental spinal motor nucleus. J. Neurophysiol. 1943, *6*, 143–152.

Lloyd, D. and H. T. Chang, Afferent fibres in muscle nerves. J. Neurophysiol. 1948. *11*. 199–208.

Maximow, A. A. and W. Bloom, A textbook of histology. W. B. Saunders, Philadelphia & London 1948. p. 200.

Pearson, A. A., The hypoglossal nerve in human embryos. J. Comp. Neurol. 1939. *71*. 21–39.

— Sensory type neurones in the hypoglossal nerve. Anat. Rec. 1943. *85*. 365–375.

PEARSON, A. A., Further observations on the intramedullary sensory type neurones along the hypoglossal nerve.
J. Physiol., Lond. 1894. *17.* 211–258.

RENSHAW, B., Influence of discharge of motoneurones upon excitation of neighboring motoneurones.
J. Neurophysiol. 1941. *4.* 167–183.

— Central effects of centripetal impulses in axons of spinal ventral roots.
J. Neurophysiol. 1946. *9.* 191–204.

REXED, B., Contributions to the knowledge of the postnatal development of the peripheral nervous system in man.
Acta psychiat. neur. scand. 1944. suppl. 33.

REXED, B. and P. O. THERMAN, Calibre spectra of motor and sensory nerve fibres to flexor and extensor muscles.
J. Neurophysiol. 1948. *11.* 133–140.

SCHOEN, R., Untersuchungen über Zungen- und Kieferreflexe. I mitteilung: der Kieferzungenreflex und andere proprioceptive Reflexe der Zunge und der Kiefermuskulatur.
Arch. exp. Path. Pharm. 1931. *160.* 29–48.

SCHOEN, R. and S. KOEPPEN, Untersuchungen über Zungen- und Kieferreflexe. II Mitteilung: Exteroceptive Reflexe und ihre wechselnde Schaltung.
Arch. exp. Path. Pharm. 1931. *160.* 343–368.

SHERRINGTON, C. S., On the anatomical constitution of nerves of skeletal muscles; with remarks on recurrent fibres in the ventral spinal root.
J. Physiol., Lond. 1894. *17.* 211–258.

SKOGLUND, S., Anatomical and physiological studies of knee joint innervation in the cat.
Acta physiol. scand. 1956. *36.* suppl. 124.

SZENTÁGOTHAI, J., Anatomical considerations of monosynaptic reflex arcs.
J. Neurophysiol. 1948. *11.* 445–454.

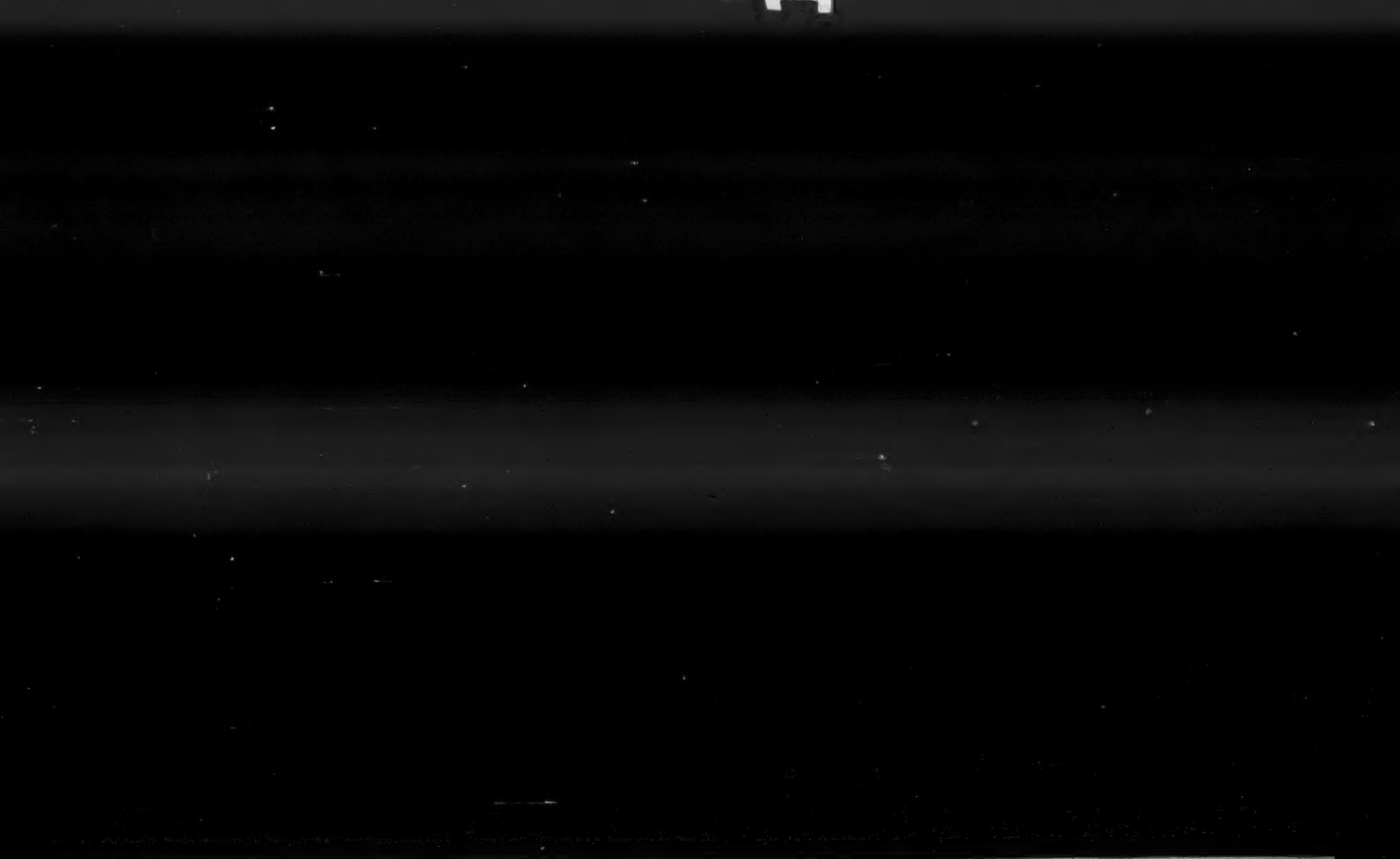
TARKHAN, A. A., Ein experimenteller Beitrag zur Kenntnis der proprioceptiven Innervation der Zunge.
Zschr. Anat. Entw. 1936 a. *105.* 348–358.

— Ueber das Vorhandensein afferenter Fasern im Nervus hypoglossus.
Arch. Psychiat., Berlin. 1936 b. *105.* 475–483.

TARKHAN, A. A. and I. ABOU-EL-NAGA, Sensory fibres in the hypoglossal nerve.
J. Anat., Lond. 1947. *81.* 23–32.

TARKHAN, A. A. and S. ABD-EL-MALEK, On the presence of sensory nerve cells on the hypoglossal nerve.
J. Comp. Neurol. 1951. *93.* 219–228.

VAN DER SPRENKEL, H. R., The hypoglossal nerve in an embryo of Erinaceus europaeus.
J. Comp. Neurol. 1924. *36.* 219–272.

VOSS, H., Zahl und Anordnung der Muskelspindeln in den oberen Zungenbeinmuskeln, im M. trapezius und M. latissimus dorsi.
Anat. Anz. 1956. *103.* 443–446.

Weddell, G., J. A. Harpman, D. G. Lambley and L. Young, The innervation of the musculature of the tongue.
J. Anat., Lond. 1940. *74.* 255–267.
Wilson, V. J., W. H. Talbot and F. P. J. Diecke, Pattern of recurrent conditioning of spinal reflexes.
Nature 1959. *183.* 824–825.
Yee, J., F. Harrison and K. B. Corbin, The sensory innervation of the spinal accessory and tongue musculature in the rabbit.
J. Comp. Neurol. 1939. *70.* 305–315.
Zotterman, Y., Action potentials in the glossopharyngeal nerve and in the chorda tympani.
Skand. Arch. Physiol. 1935. *72.* 73–77.
— Specific action potentials in the lingual nerve of cat.
Skand. Arch. Physiol. 1936. *75.* 105–119.